THESIS

REFORESTATION PRACTICES AND MICROSITE EFFECTS ON THE PERFORMANCE OF CONTRASTING SYMPATRIC TREE SPECIES: A CASE-STUDY FOR ADAPTIVE SILVICULTURE

Submitted by

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ABSTRACT

REFORESTATION PRACTICES AND MICROSITE EFFECTS ON THE PERFORMANCE OF CONTRASTING SYMPATRIC TREE SPECIES: A CASE-STUDY FOR ADAPTIVE SILVICULTURE

In the central-southern Rocky Mountain region, warming climate in low-elevation Engelmann spruce forests may limit future viability of spruce but favor sympatric species like ponderosa pine, prompting consideration of both species in adaptive reforestation efforts. We used a planting experiment to systematically evaluate survival and root growth of these contrasting species to microsite conditions resulting from silvicultural regeneration treatments in a spruce forest on the Uncompahgre Plateau, Colorado. Our assessment targeted the effects of varying levels of canopy cover generated by different regeneration treatments, paired with and without microsite shelter from coarse woody debris. For explaining survival, we also considered the potential for covarying microsite influences of vegetation, soil, or litter cover, soil moisture and depth, surrounding natural tree regeneration, and seedling size. Survival of pine was twice that of spruce, but the relative effects of microsite variables were similar, possibly due to the severe drought during our study and the stress of first-season establishment. Coarse woody debris shelter benefitted survival of both species, likely from shading of succulent stem tissue and improved soil moisture retention. Influences of canopy cover were comparatively indistinct overall, which may reflect reduced capacity for temperature and moisture buffering on extremely dry sites. Survival was also strongly negatively affected by seedling height, suggesting a potential benefit of lower above-to-belowground biomass ratios for establishment in stressful

environments. Root growth was seemingly limited by light for both species in the most dense, unharvested canopy environments, and for pine in coarse woody debris shelter. Our results imply that adaptive reforestation efforts in similar environments should consider more drought-adapted, sympatric species as viable alternatives or supplements to moisture-dependent species at their current lower range limits. Additionally, our results show that first-season seedling survivorship is strongly dependent on facilitating influences of adjacent, non-living shelter, especially compared to canopy cover effects, and seedling development prior to outplanting, favoring lower shoot-to-root ratios.

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CHAPTER 1: REFORESTATION PRACTICES AND MICROSITE EFFECTS ON THE PERFORMANCE OF CONTRASTING SYMPATRIC TREE SPECIES: A CASE-STUDY FOR ADAPTIVE SILVICULTURE

1.1 Introduction

Research related to adaptive management and adaptive silviculture practices is motivated in part by the need to support forestry professionals with systematic evaluation of relevant management options for effectively responding to anticipated effects of climate change on forest dynamics (e.g., Kemp et al. 2015, Sousa-Silva et al. 2018). Considerable attention has been given to potential climate change-related impacts on forest composition, structure, and function, but there is a need for more thorough investigation of the mechanisms of potential impacts and the opportunities for different silvicultural approaches to address these mechanisms (Keenan 2015; Fahey et al. 2018). These concerns have in part been resolved through development of conceptual and integrative frameworks for practical implementation of adaptive management ideas (DeRose and Long 2014), and are increasingly incorporated into operational-scale field trials of different silvicultural strategies and tactics (e.g., Nagel et al. 2017; Yousefpour et al. 2017; Halofsky et al. 2018; Fahey et al. 2018). However, adaptive approaches seek to manage uncertainty surrounding the extent and outcomes of environmental change, which are dependent on ecological responses and feedbacks occurring at local to regional geographic scales and at different time scales (Jacobs et al. 2015; Messier et al. 2016; Fischer 2018). Consequently, there is a need to better understand mechanisms of uncertainty and change as they relate to environmental and practical concerns in local- and regional-specific management applications, and at relevant time scales (Keenan 2015; Kemp et al. 2015; Lawrence 2017; Fahey et al. 2018;

Sousa-Silva et al. 2018). More specifically, to effectively manage toward desired future conditions in the context of uncertainty (or within envelopes of acceptable conditions; Matonis et al. 2016; Golladay et al. 2016), silviculture practitioners will in part rely on continuous, case-study scale research which provides robust estimation of outcomes relevant to silvicultural strategies and practices in local- and regional-specific environments. A necessarily iterative process (e.g. Lawrence 2017; Halofsky et al. 2018) given the gradual unfolding of climate change effects, case-study applications evaluating mechanisms of change in forest dynamics and the influence of silvicultural practices can be time- and resource-efficient contributions in this regard.

Regeneration and reforestation (hereafter reforestation) practices are among the foremost concerns in adaptive silviculture, especially given uncertainty in the pace and extent of climate change and species' autecological and synecological responses to varying degrees of environmental change (Messier et al. 2016; Nolan et al. 2018; North et al. 2019). In this way, adaptive reforestation practices, including but not limited to regeneration treatments and planting practices, are essential for ensuring forest cover and function through securing new cohorts of trees. This requires managing for the greater sensitivity of juvenile trees to limiting conditions that define a species' viability (Pulliam 2000; Máliš et al. 2008), which may be exacerbated or diminished with climate change impacts (e.g., Bell et al. 2014). Specifically, while the climate-related processes that could drive changes to forests at landscape scales are complex, the restrictive nature of conditions suitable for seedling establishment relative to adult survival suggests regeneration failures are a plausible mechanism for changes in species distributions and forest cover and function as a result of climate change (Mok et al. 2012; Bell et al. 2014; Copenhaver-Parry et al. 2017). These concerns are likely to be amplified in areas that are

marginal relative to the general distribution of a species (Bell et al. 2014; Dobrowski et al 2015), such as lower and upper elevation range extents (Kroiss and HilleRisLambers 2015), but will depend in part on species-specific adaptations to abiotic extremes or variability (e.g., Ibáñez et al. 2007; Larson and Funk 2016). In these areas, adaptive approaches to reforestation may therefore include managing for a diversity of species with different adaptations to current or expected environmental conditions, namely climate (Aitken et al. 2008; Hof et al. 2017; Guldin 2019). These concerns underscore the need for local and regional reforestation efforts to better account for biophysical microsite influences (Lembrechts et al. 2018), especially those affected by silvicultural practices, for the various species (mixes) which silviculture seeks to regenerate (Chmura et al. 2011; Larson and Funk 2016; Anderson and Puettmann 2017; Nolet et al. 2018; Guldin 2019). Consequently, there is a need to evaluate reforestation options and tools in terms of species responses to microsite conditions, especially those that relate to components of the silvicultural regeneration treatment environment (Grossnickle 2018). Reforestation options are therefore critical considerations in adaptive silviculture that is responsive to climate change, as these provide the basis for ensuring forest cover and function, implying the need to more precisely account for microsite influences on performance of species of interest, especially in sensitive marginal distribution areas.

Adaptive silviculture approaches to reforestation in the central-southern Rocky Mountain region will likely need to consider greater frequency of growing season drought conditions resulting from reduced snowpack and increased summer temperatures in the future (Lukas et al. 2014). These anticipated changes may restrict survivorship of mesic, high-elevation species, especially at their lower elevation range (marginal) limits (Conlisk et al. 2017; Kueppers et al. 2017), while favoring or expanding that of more xeric, montane species (Rehfeldt et al. 2014;

Elsen and Tingley 2015). Yet, silviculture provides opportunities to mediate the pace and extent of climate-induced changes in these forest communities, especially through manipulating forest structure and composition. Management of structural conditions like density of canopy trees can influence microsite temperature and moisture relations for juvenile trees (Chen et al 1999; Aussenac 2000; Gray et al. 2002; von Arx et al. 2013; De Frenne et al. 2013; Davis et al. 2019). In this way, silvicultural practices directly influence the presence and distribution of niche conditions for different species which are desired for reforestation. However, adaptive reforestation approaches in marginal distribution spaces in this region must account for the precise nature of both high-elevation and montane species' responses to microsite conditions generated by silvicultural treatments. It is therefore useful to evaluate the performance of different species, with contrasting silvics and diverging expectations of future viability, in reforestation efforts relative to microsite influences in regeneration environments, especially those arising from silvicultural regeneration treatments.

In the central-southern Rocky Mountain region, and locations like the Uncompahgre Plateau in particular, these concerns are present in the management of regeneration in low-elevation Engelmann spruce (*Picea engelmannii*; hereafter "spruce") forests. Spruce has been historically difficult to regenerate in this region with both even-aged (e.g. clearcut regeneration treatments) and uneven-aged, selection-based systems (Alexander 1987; Davy 2016). However, silvicultural tactics used to alleviate stress of extreme temperatures and moisture availability, such as facilitating shade or scarifying seedbeds to reduce competition with other vegetation, have generally resulted in higher survival and seedling densities than practices not specifically addressing those driving stressors (Day 1963 and 1964; Ronco 1967 and 1970; Alexander 1987). For instance, research on opening sizes and tree-density related effects from silvicultural

practices suggests that spruce typically favor low (Hill et al. 2018) to intermediate (Alexander et al. 1985; Alexander 1987) amounts of canopy cover in selection-based regeneration treatments, or artificial or topographic sheltering in the absence of canopy cover (e.g. clearcuts; Alexander 1966 and 1984; Jacobs and Steinbeck 2001). Recent modeling efforts suggest that, at lower elevations of its range, climate warming will result in spruce population declines (Conlisk et al. 2017; Kueppers et al. 2017). Similarly, bioclimate modeling, inclusive of Uncompahgre Plateau, suggests that climate conditions may effectively preclude spruce persistence after 40-50 years (Rehfeldt et al. 2015). However, spruce is a particularly important species locally on the Uncompahgre Plateau for conservation efforts via (adaptive) forest management, due to its value as a timber species, role in wildlife habitat (e.g. elk), and aesthetics and recreation (CFRI 2017).

Ponderosa pine (*Pinus ponderosa*; hereafter "pine") is a sympatric species on the Uncompahgre Plateau which may be better adapted to these forecasted changes, especially for its superior ability to withstand drought and better leverage warmer conditions for growth (e.g., Rehfeldt et al. 2014; Carroll et al. 2017). However, it is unclear to what extent pine's characteristic occupation and dominance of comparatively moisture limited montane forests in this area translates into a relative advantage in actively changing low-elevation spruce forests, specifically for young seedlings used in reforestation efforts (e.g., Petrie et al. 2016). Because of anticipated climate change effects in these low-elevation spruce forests, adaptive silviculture in these areas might consider reforestation options including both species. However, there are no examples that we are aware of which systematically examine the performance of these candidate reforestation species relative to the influences of silvicultural practices and resulting microsite conditions in these forests.

Spruce is a highly moisture dependent species (reviewed in Hill et al. 2018), and young seedlings may be acutely dependent on microsite influences that facilitate moisture availability in low-elevation forest stands (Conlisk et al. 2017; Kueppers et al. 2017) on the Uncompahgre Plateau or similar environments in the central-southern Rocky Mountain region. Silvicultural regeneration practices which retain sufficient canopy cover (e.g. uneven-aged systems) and coarse woody debris on the forest floor may help create regeneration niches with relatively high moisture availability, favored by spruce (e.g., Rehfeldt et al. 2015; Davy 2016). Conversely, pine may be less influenced by such practices (Sheppard et al. 2006) in these spruce stands, particularly because pine regeneration potential may increase with elevation, as documented repeatedly after disturbance events (e.g. Stein 1988; Puhlick et al. 2012; Dodson and Root 2013; Chambers et al. 2016; Rother and Veblen 2016). Additionally, direct results generated by silvicultural treatments, like changes in canopy cover or woody debris microsites, affect seedling performance concurrently with other features of seedling microsite environments (e.g. Gray et al. 2002; Chmura et al. 2011; Anderson and Puettmann 2017). These features may include soil characteristics (e.g. moisture, texture, depth) and soil cover by other vegetation or dead organic matter (i.e. litter or debris). Accounting for the relative effects in the seedling microsite environment, which can covary with those generated by silvicultural treatments, will be an essential part of informing reforestation options in these forests (Larson and Funk 2016; Lembrechts et al. 2018).

To address this issue we established a planting experiment in a low-elevation spruce forest on the Uncompahgre Plateau to assess seedling establishment of pine and spruce under different silvicultural reforestation practices, and covarying biophysical microsite influences. Our objective in this study was to determine the relative effects of silvicultural treatment

variables designed to facilitate spruce regeneration, namely varying levels of canopy cover and coarse woody debris shelter, and other microsite variables on the early survival and growth of both species to inform reforestation strategies and tactics in an adaptive management context. The driving questions for the experiment were focused on evaluating reforestation options from both a species and a silvicultural practices perspective, that is: (1) how does survival and growth of spruce and pine compare and vary with canopy cover, coarse woody debris shelter, and other concurrent microsite variables? And, (2) what are the effects of canopy cover and woody debris on survival and growth of spruce and pine, relative to other microsite variables? We hypothesized that spruce would show strong sensitivity to influences on moisture availability, whereas pine responses would not be as sensitive. Specifically, we expected that spruce survival would benefit from intermediate to dense canopy cover and coarse woody debris. In contrast, we expected that pine survival would be favored in intermediate to low canopy cover and show relative indifference to coarse woody debris shelter, except in the most exposed (open) canopy environments. Both species were expected to be sensitive to influences on moisture availability like soil moisture, competing vegetation, and retention effects of litter and debris cover. Pine was expected to show greater sensitivity to light availability. Lastly, we expected growth to benefit from intermediate to low canopy cover, but to be indifferent to coarse woody debris shelter. Our results contribute new knowledge and insight into the effects silvicultural treatments on sympatric species with differing silvics in terms of their microsite environments, with implications for adaptive silviculture.

1.2 Methods

1.2.1 Study Area

We established our comparative planting study of Engelmann spruce and ponderosa pine in May 2018 in an active timber sale area about 3.7 km northwest of Columbine Pass on the Uncompahgre National Forest, in southwest Colorado (~ 38° 26' N, 108° 25' W; Figure 1). The sale area covered an elevation gradient from 2717-2792 m in a spruce-dominated forest near the upper elevational extent of the Uncompahgre Plateau, a landform which rises from the surrounding valleys and is largely physiographically distinct from the surrounding mountains (Hedge et al 1968). Topography of the sale area is predominantly northerly in aspect and flat, as slopes are typically less than 10%. Some slopes as high as 30% occur in at edges of the sale area which approach ephemeral stream bottoms (USDA NRCS 2018). Soils are almost exclusively sedimentary-derived complexes which are characterized by minimal organic layers, and rapidly-draining sandy and clay loam soils with low water holding capacity (Hughes et al. 1995; USDA NRCS 2018). Bedrock may occur only 10-30 inches below the surface in these soils, which can present substantial limitations to productivity in some areas (Hughes et al. 1995). While geospatial soil data (USDA NRCS 2018) do not suggest varied substrate at coarse resolution, visual observations in the area clearly suggest some locations are dominated more than others by continuous rock material visible at and above the soil surface. Engelmann spruce is the dominant tree species in the study area, but the Uncompahgre Plateau represents a regional physiographic margin of its distribution, due to the geographic separateness of the Plateau from surrounding spruce forests and the low elevations of these forests relative to the typical altitudinal range of spruce in the central Rocky Mountains (Alexander 1987). Ponderosa pine is a co-dominant overstory species in northern portions of the study area and becomes the dominant

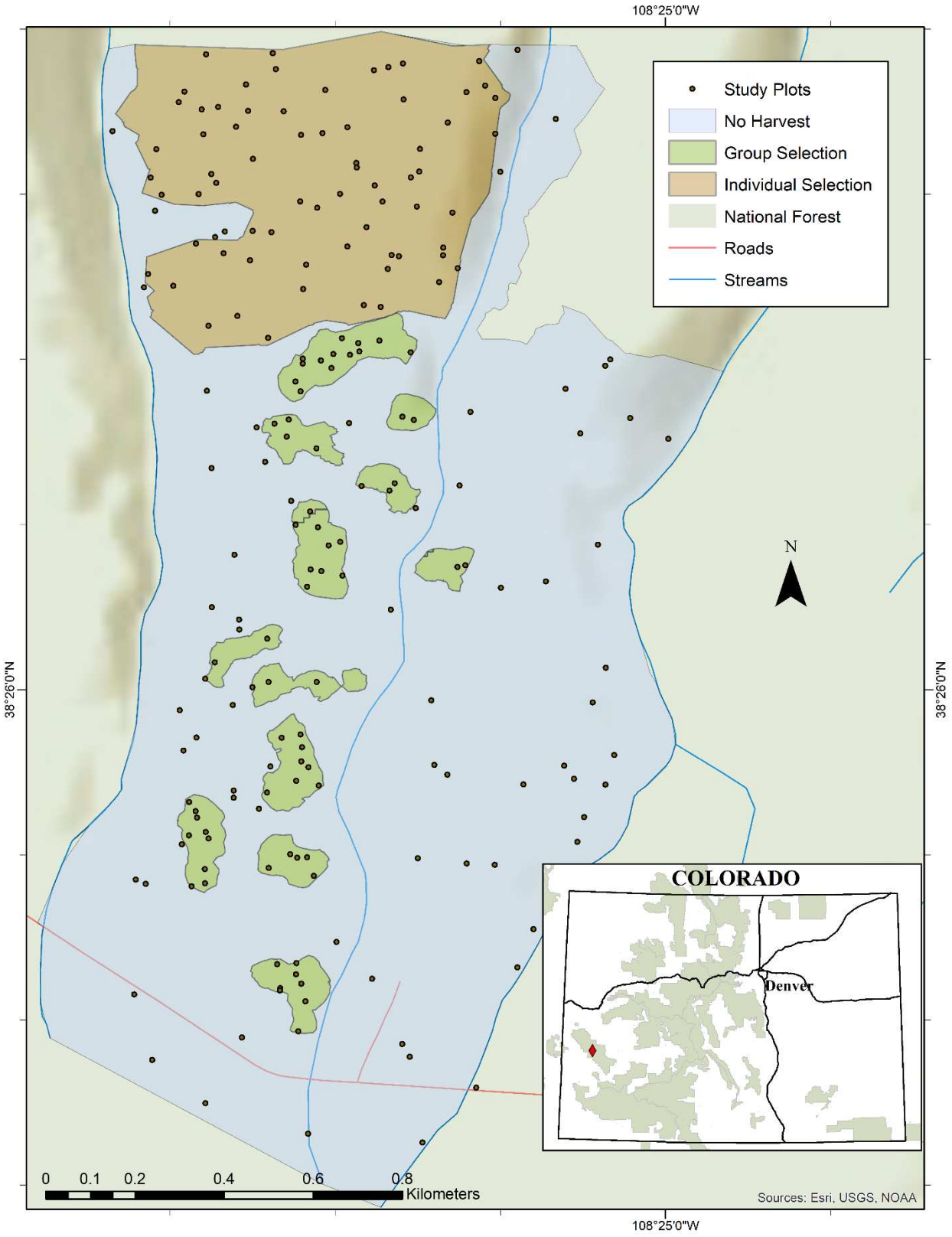

Figure 1. Detail map and inset locator map of the study area, which encompasses part of the active timber sale in which this planting study was established. The study area specifically was located between two ephemeral stream

bottoms bordering portions of the timber sale which had been harvested at the time of this study. Harvest areas (data via Todd Gardiner, personal communication, April 11, 2018) are indicated by light green shading (group-selection treatment) and light brown shading (individual-tree selection treatment). Unharvested areas were used for a no treatment comparison and are shaded in blue, surrounding harvest openings. Elevation of the area ranges from 2717-2792 m, and slopes are largely < 10% with northerly aspects. Plots in our study are indicated by the circular symbols; two seedlings of each species were planted at each plot location, with one planted in coarse woody debris shelter and one planted without. All data, unless otherwise indicated, retrieved from the USDA NRCS Geospatial Data Gateway (USDA NRCS 2018).

species at lower elevations. Pockets of Douglas-fir (*Pseudotsuga menziesii*) are also present, and aspen (*Populus tremuloides*) are abundant in both the canopy and understory. Though subalpine fir (*Abies lasiocarpa*) is also a ubiquitous associate of spruce in the area, mortality of canopy fir at the time of study was close to 100% due to previous spruce budworm activity.

Data from the nearest weather station, at Columbine Pass, indicate that the area receives about 84.5 cm annual precipitation on average (Figure 2; 1987-2017 data from SNOTEL site 409, ~ 2,870 m, 38°25' N, 108°23' W, https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=409), the majority of which arrives in the form of snow. In contrast, growing season (May-September) precipitation accounts for only about 26% of annual totals and arrives predominantly in July-September. Temperatures (Figure 2) typically reach their annual average maximum (30.7° C) in July or August and average near 12.8° during the growing season. Winters are cold, and the average annual winter temperature is approximately -1.0° C. Conditions during our study period (May-October 2018) diverged considerably from these average conditions (1987-2017), being warmer and drier in nearly every month on average (Figure 3). Notably, average temperatures over the growing season period were 1.6° C higher, and precipitation, totaling only 7.87 cm, was 36% of the average over this period. In addition, monthly precipitation accumulation was highly variable, with over 50% coming during July 2018 and zero accumulation recorded in June 2018. Compounding these warmer and drier growing season conditions, winter temperatures and precipitation (October 2017-April 2018) saw precipitation accumulations only 38% of average

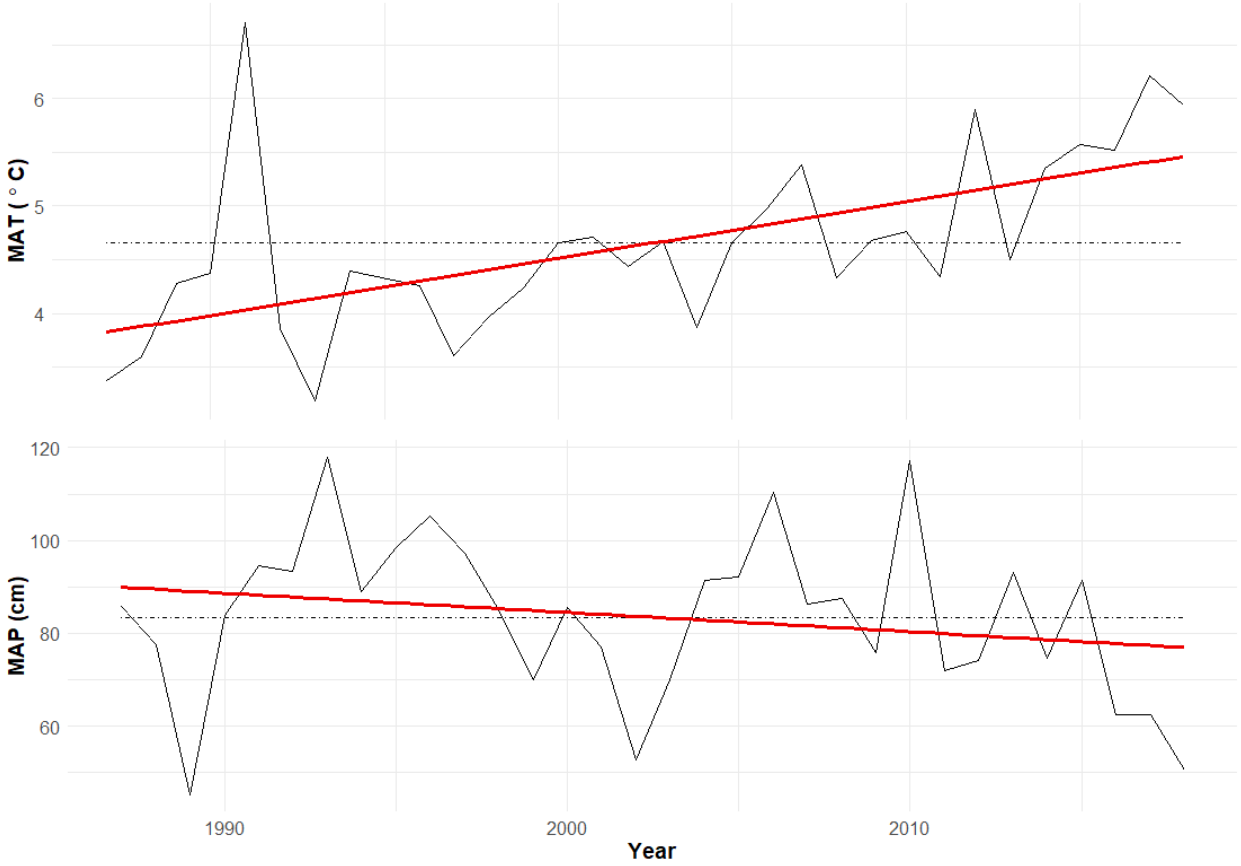

Figure 2. Mean annual temperature (MAT; top panel) and mean annual precipitation (MAP; bottom panel) near the study site for 1987-2018, inclusive of our study period (May-October 2018). Dashed lines indicate mean conditions for the period 1987-2018, and red lines represent the linear trend over this period. Weather conditions for our study period diverged sharply from these average conditions (see Figure 3) but are more consistent with the linear trends displayed here and expected for this region (Lukas et al. 2014). Climate data were downloaded from the Columbine Pass USDA NRCS SNOTEL site (site 409, ~ 2,870 m, 38°25' N, 108°23' W, https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=409).

and temperatures 2.28° C higher on average (Figure 3). These conditions, particularly higher average winter and annual temperatures, may reflect changes in climate which are predicted to occur in this region (Lukas et al. 2014).

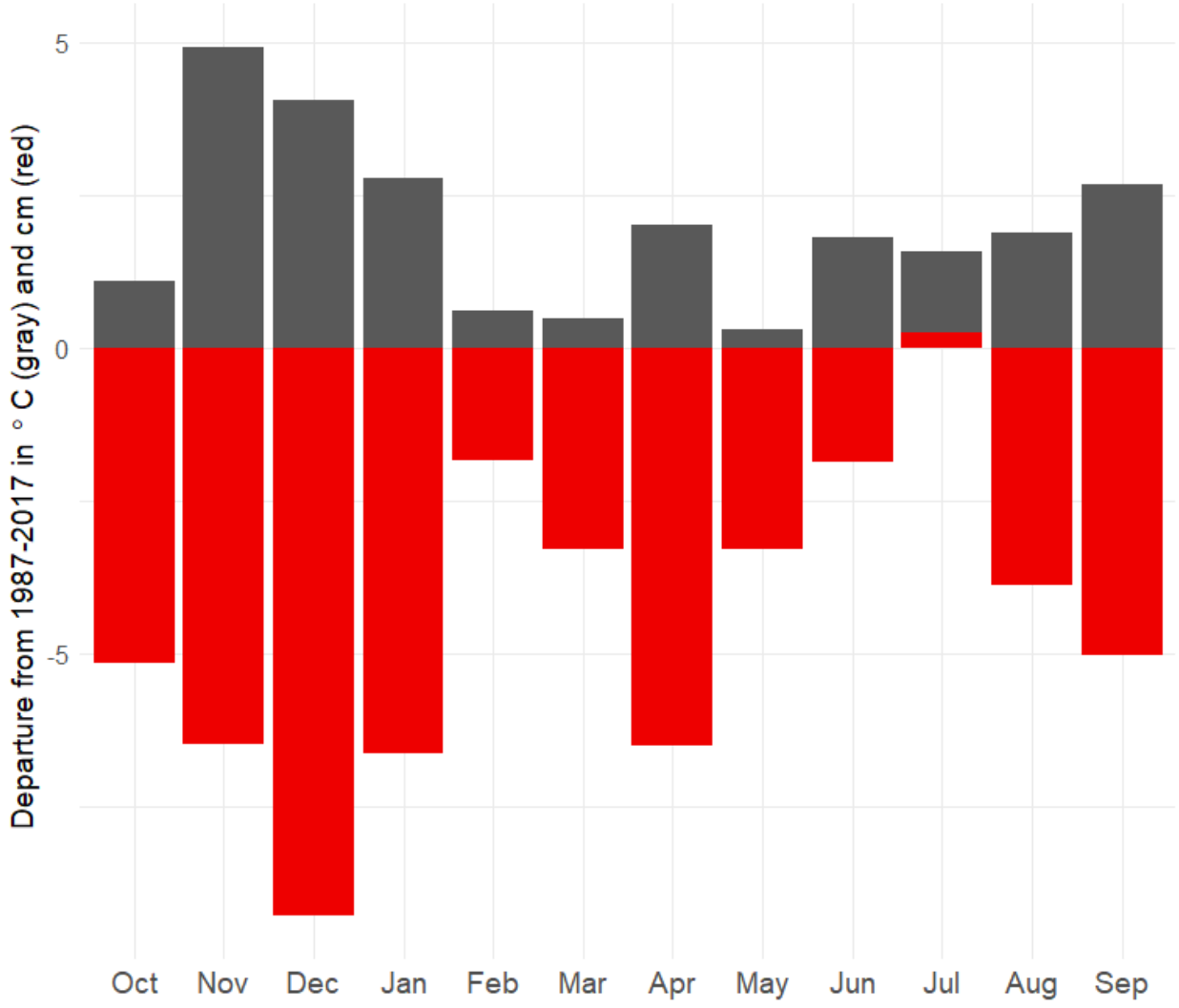

Figure 3. Temperature (gray) and precipitation (red) deviations from average conditions near the study site (1987-2017) for the 2018 water year (October 2017 – September 2018), inclusive of our study period growing season (May-September 2018). All mean monthly temperatures were above average conditions (gray bars), and all months except July were lower in precipitation accumulation than average conditions (red bars). Notably, zero precipitation was recorded in June 2018. Climate data were downloaded from the Columbine Pass USDA NRCS SNOTEL site (site 409, ~ 2,870 m, 38°25' N, 108°23' W, https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=409).

1.2.2 Experimental Design and Measurements

We randomly located plots within the study area (Figure 1) for planting tree seedlings and examining the effects of varying levels of canopy cover, woody debris, and vegetation and soil microsite (~ ≤1 m^2; Gray and Spies 1997) characteristics on the performance of planted seedlings. Plots were distributed evenly within three canopy environments resulting from

silvicultural regeneration treatments (or no treatment) and representing contrasting levels of canopy (or, overstory) cover for tree seedlings. Point generation for plots and definition of treatment environments and strata was accomplished using geospatial data processing tools available in ArcMap 10.5.1 (ESRI Inc., Redlands, CA, USA). Sampled canopy treatment environments included: (1) group-selection openings with little to no canopy cover; (2) individual-tree selection areas, with variable canopy cover; and (3) unharvested areas with continuous canopy cover (Figure 1). Group-selection openings in our study area (~ 6.8% of total area; 12 openings, ~ 1.13 ha each) typically reflected complete overstory removal, though often a few legacy canopy trees were retained, in addition to some advance regeneration. Moreover, these openings were heterogeneous in shape and size, but mostly long and narrow (Figure 1), resulting in edge effects dominating relative to opening interiors. Ground cover in these openings was a mix of juvenile trees (especially aspen), herbaceous vegetation, varying sizes of woody debris and litter, and bare mineral soil. The individual-tree selection treatment area (~ 18.5% of total area) varied from location to location within the treatment in residual canopy species proportions (namely spruce, pine, Douglas-fir, and aspen) and structure (e.g. groups of smaller trees like spruce and aspen, or single large Douglas-fir, pine, or spruce). Within this treatment area, ground cover ranged from large inter-tree spaces with woody debris and rock to shrubby and herbaceous vegetation-dominated interspaces. Finally, our non-harvested environments (74.7% of total area) were highly variable in canopy tree density, but were primarily dominated by spruce and dead subalpine fir in the canopy. Considerable variation in vertical structure was also present, with a strong presence of juvenile and intermediate canopy trees. Ground cover was often vegetated, though we encountered many sections of bare mineral soil, rock, and debris. While plots were distributed based on these categorizations of canopy

cover, we also sought to evaluate species' responses over a continuous gradient to better estimate canopy effects. We accomplished this by sampling basal area of canopy trees and openness of the canopy/sky with hemispherical photographs (see below for details).

Based on prior observations, we determined that the northern, slightly lower elevation section of the study area included greater proportions of ponderosa pine and more exposed rock at the ground surface. We therefore chose to stratify our plot distribution based on division of the total area by an elevation band close to this apparent transition from higher to lower elevation in the study area. The resulting strata each covered roughly 200 m of elevation range, and our stratification of plots was made according to the proportion of total study area of each stratum, about 2/3 and 1/3 for the higher- and lower-elevation stratums, respectively. Plots were deemed unsuitable if the random location was not conducive for planting. Criteria for planting unsuitability included bedrock, stumps, skid roads and thick debris piling from harvest operations, and excessive depressions or mounds relative to the surroundings usually resulting from harvest operations or windthrow. Plots were also unsuitable if the point fell outside the boundary of the opening type for which it was generated (i.e. if the geospatial definition did not correspond well to the actual harvest boundary). If a point failed to meet the criteria above, it was shifted 5 m in a randomly selected cardinal direction. If this procedure failed to produce a suitable plot location, the plot was discarded. In total, 206 plots were established in the study area, 69 in both group-selection and non-harvested canopy environments, and 68 in the individual-tree selection canopy environment.

Plot layout was designed to accommodate seedling plantings for both species and measurements of microsite biophysical variables potentially affecting the performance of each seedling in a given plot. The design was structured around a plot center produced by our

randomly generated points (see preceding details). Around each plot center, a 1 m^2 area was established, with each side of the square set perpendicular to the four cardinal directions and corners of the square serving as seedling planting locations (Figure 4). To achieve our objective of assessing the microsite effects of coarse woody debris ("CWD") shelter on seedling performance within each canopy type, we created microsite shelter with coarse woody debris placed on the north side of each plot square (Landis 2010; Davy 2016). We chose the nearest piece of CWD to plot center which had a diameter of at least 7.6 cm, or 75% of the minimum target height (10.2 cm; Richard Gilbert, personal communication, July 20, 2018) of our seedlings. We chose this size to ensure that the debris provided sufficient sheltered (shaded) microsite conditions for planted seedlings (e.g. Germino et al. 2002; Maher et al. 2015). Data from prior work on the effects of CWD for spruce regeneration in harvest openings in nearby sites suggests that temperatures are significantly moderated on the north side of CWD in this area, keeping temperatures 5.5°C below ambient conditions on average; this difference significantly enhanced spruce germination in the study (Davy 2016). If the nearest piece of CWD meeting the size criterion above was shorter than the plot edge (1 m) or was unmovable (e.g. trapped under other logs, overly decayed, or too large to feasibly move), we chose the next nearest piece that was within 2.5 cm diameter of the original piece. Instances of these exceptions were rare, occurring at only about 5% (11) of plots. The chosen piece of debris was laid on the north side of the plot square and measured at three equidistant locations (0 m, 0.5 m, 1 m) along the plot edge to determine its average height above the ground surface in order to assess whether size of debris had an influence beyond the categorical presence of the CWD microsite effect.

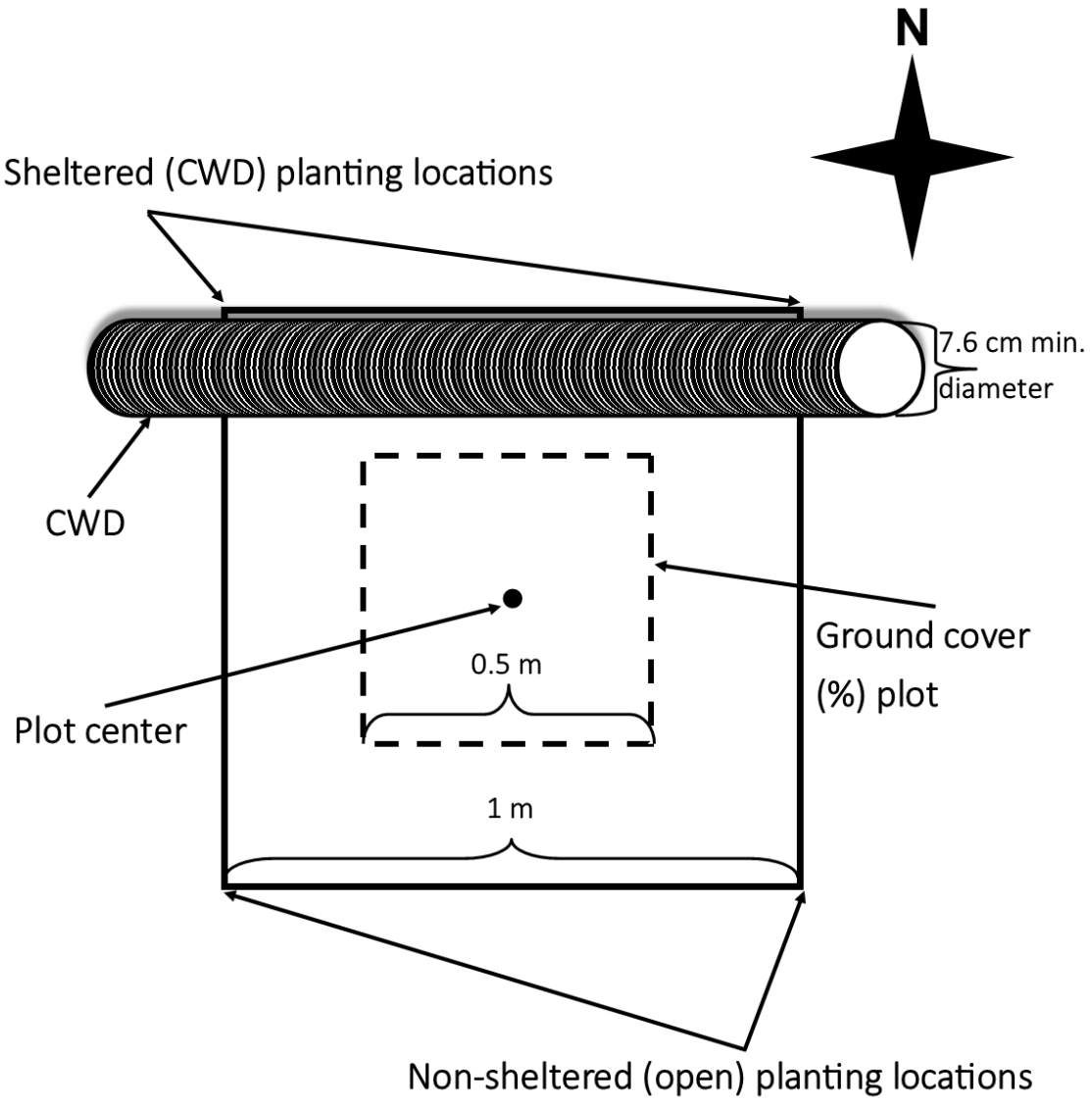

Figure 4. Plot design structured around randomly generated points (plot center). Plots were 1 m2, oriented with sides perpendicular to cardinal directions. Coarse woody debris, at least 7.6 cm diameter, were used to create microsite shelter for planting at the north edge of plots. One seedling of each species, Engelmann spruce and ponderosa pine, was planted in a microsite location and non-microsite (open) location, at the corners of the plot. Subplots (0.5 m2) were used to sample vegetation (by life-form), soil, and litter/debris cover around plot center. From plot center, basal area (m2 ha-1) of overstory trees (> 5 cm DBH) was sampled with variable radius plots, and counts of juvenile trees (<5 cm DBH) were tallied by 0.5 m height classes in 3.6 m radius fixed plots. Soil cores were also taken at plot center to estimate soil volumetric moisture content at each plot, and hemispherical photographs taken at plot center (30 cm height above ground surface) to precisely estimate canopy cover, or sky exposure, experienced by seedlings.

We planted 824 spruce and pine seedlings (412 of each; 2 per species per plot) in late June 2018 over the course of five days. Seedlings were 1-0 containerized (108.2 cm^3 plug volume; Richard Gilbert, personal communication, July 20, 2018) stock grown at U.S. Forest Service facilities (Bessey Nursery, Halsey, Nebraska). Seedlings were randomly planted on plot corners (Figure 2), with one of each species planted with CWD microsite shelter (north side of CWD on the north edge of a plot), and one of each planted without CWD shelter (south side of a plot). Hoedad tools were used to remove surface vegetation and debris (scalp) in a circle of ~15 cm radius at each planting position (USDA FS 2002; Landis 2010), and subsequently used to plant each seedling. At the time of planting we measured diameter at root collar (DRC) and height from DRC to the top of the terminal bud for each seedling. Size was measured to account for the potential effects of planting stock size on survival (e.g., Davis and Jacobs 2005; Grossnickle and MacDonald 2018).

To assess the potentially covarying influences of forest structure, ground cover, and soil moisture on seedling performance, we sampled these characteristics at each plot center. Counts of juvenile trees within a fixed area plot of 3.6 m radius from plot center were recorded for 0.5 m height classes. Juvenile trees were considered those less than 5 cm diameter at breast height (DBH), and can be either competitive or facilitative influences for seedlings (e.g., Callaway 1998). Density of canopy, or overstory trees (e.g., Alexander 1987; Shepperd et al. 2006) was sampled with variable-radius plots using a 2.30 basal area (m^2 ha^{-1}) factor prism to tally trees greater than 5 cm DBH by species. Heights, a measure of local productivity, were also recorded for each overstory tree. Percent cover of vegetation in major life form groups (forb, shrub, graminoid, moss), bare soil, woody debris and litter, and rock were estimated in 5% increments within a 0.5 m^2 quadrat situated about plot center. Cover measurements were used to estimate

potential productivity within a given microsite (e.g., Day 1963 and 1964; Newsome et al. 2016; Bonnet et al. 2005; Puhlick et al. 2012; Fleming et al. 1998; Callaway et al. 1996; Ouzts et al. 2015; Pinto et al. 2012). Finally, soil cores (0-20 cm) were extracted using a 2.2 cm dia. corer from each plot center during 3 consecutive days (same weather conditions) in July 2018 to estimate relative moisture availability at a given plot location (Day 1963; Kolb and Robberecht 1996; Puhlick et al. 2012; Gill et al. 2015; Feddema et al. 2013). Depth to restriction was recorded in all plots where the 20 cm depth was not possible. Soil samples were weighed in the field, bagged, and oven dried at 105° C to constant mass (Saxton and Rawls 2006)for determining gravimetric moisture content (percentage of dry weight). We used the dimensions of the soil core to calculate soil bulk density and subsequently estimate volumetric water content (VWC).

To obtain more precise estimates of the effects of canopy tree density on seedling environments (Chen 1997; Feller 1998; Keyes et al. 2007; Holmgren et al. 2011; von Arx et al. 2013), hemispherical photographs were taken at plot centers using a DSLR camera, mounted on a self-leveling mechanism equipped with a fish-eye lens (24MP DSLR Compact OMount, Regent Instruments, Inc., Québec, Canada), in pre-dawn and overcast sky conditions to ensure adequate contrast between vegetation and sky. Photos were taken at about 30 cm height above the ground to represent conditions experienced by planted seedlings with greater direct relevance than higher positions above the ground (e.g. >1 m; Davis et al. 2019). Photographs were processed using WinsCanopy Pro 2016a software (Regent Instruments, Inc., Québec, Canada) to obtain estimates of percent openness of the sky (% of sky), which can be representative of available photosynthetically active radiation and exposure to atmospheric fluctuations in temperature and moisture. Openness, unlike some alternative measures of canopy cover,

accounts for unequal projection of hemisphere elements captured by a fish-eye lens (e.g., Frazer et al. 1997; Glatthorn and Beckschäfer 2014; Hall et al. 2017).

1.2.3 Seedling Performance: Survival and Root Growth

Our measures of seedling performance relative to planting environments included survival and root growth, estimated by total root biomass (Grossnickle 2005a; Grossnickle 2012). We chose to specifically evaluate survival and root growth as measures of performance of each species in the first season following planting, since both are indicative of seedlings establishing in the outplanting environment and thus are indicative of future viability (e.g. Davis and Jacobs 2005; Grossnickle 2018). While growth or biomass accumulation can be indicative of seedling establishment in the outplanting environment (Davis and Jacobs 2005; Grossnickle 2005a and 2012; Kolb and Robberchet 1996), specific conditions favoring growth often do not correspond directly to influences on survival (Lopushinsky and Beebe 1976; McTague and Tinus 1996; Rose et al. 1997; Pinto et al 2012). Plots were revisited one month after planting and again at the end of October 2018 to assess seedling survival. Seedlings with green foliage and succulent tissue at our final assessment were considered survivors. All surviving seedlings were carefully excavated with shovels in October 2018, placed in plastic bags, and cold stored for transport back to lab facilities in Fort Collins, CO to process for biomass sampling. Biomass sampling consisted of washing soil from the roots of each seedling, separating aboveground and belowground (root) biomass at the root collar, and bagging each component for oven drying (e.g., Balisky and Burton 1997). Samples were dried in ovens at 55° C to constant mass, about 3 days, and subsequently weighed for dry mass.

1.2.4 Statistical Analysis

1.2.4.1 Survival

We sought to analyze seedling survival of each species relative to the effects of canopy cover (density) resulting from silvicultural regeneration treatments (or none), shade or shelter provided by CWD (or none), and potentially concurrent influences by microsite characteristics of ground cover, soil moisture and depth, other juvenile trees, and seedling size attributes. Our analysis consisted of first using non-parametric permutation tests (*rcompanion* package in R, Mangiafico 2019) to assess survival of each species and microsite variables for potential differences between each of the three sampled canopy environments (pairwise comparisons; significance set at $\alpha = 0.05$). We began with this step to understand potential differences in survival responses and observed microsite conditions within each canopy environment based on our sampling design and to facilitate interpretation of treatment type and microsite effects on seedling survival. However, for a more precise understanding of the range of microsite influences present within and across treatment (or none) environments, we sought to explain survival relative to a gradient of conditions across the study area. Therefore, we subsequently used generalized linear models with a logit link and binomial distribution (i.e. logistic regression) to model survival. For these logistic models, a success was defined as survival to the point of our final assessment in October 2018. Each species (spruce and pine) was modeled separately, given their contrasting silvics and expectation that they would respond differently to microsite conditions like shade, moisture, and competition. Our objective in this regard was explaining observed variation in survival for each species given microsite conditions, and developing classification metrics for predictive (survival versus non-survival) inference. Because our sampling design included paired observations for a species at each plot location

(survival nested within plot), we used mixed effects to account for non-independence inherent in this design (Harrison et al. 2018). Specifically, we allowed for estimation of random intercepts for each plot. All models were developed with the *lme4* package (Bates et al. 2015) in R (version 3.4.1, R Core Team, 2017).

Furthermore, since our research questions and design primarily concerned the influences of canopy cover levels and CWD shelter, we included variables for these components *a priori* in all models. For each component, our data contained two highly correlated measurements. We used biological reasoning, interpretability, and corrected Akaike's Information Criteria (AIC_c; Burnham and Anderson 2002) from univariable model statements to choose among correlated variables. We considered models within $\Delta AIC_c < 6.00$ to have similar support (Harrison et al. 2018). For an estimate of canopy cover variability, descriptive of variation across and within regeneration treatments and the no treatment comparison, we chose to use the openness variable obtained from processing our hemispherical photographs rather than sampled overstory basal area (Pearson's $r = -0.82$). This decision was based on the more direct interpretation of openness as a measure of how much shade a seedling received since it reflects the canopy environment resulting from tree heights, and crown shapes and porosity of foliage, which is not directly evident from basal area estimates. Additionally, support for the openness variable was higher than that for basal area ($\Delta AIC_c = 6.10$). We also considered the potential for a non-linear relationship of survival with openness (e.g. Holmgren et al. 2011), but found that support was similar ($\Delta AIC_c = 1.93$) so chose to retain only a linear term. As a measure of the influence of CWD shelter, we chose to proceed with a two-level factor variable rather than the continuous measure of CWD average size (Pearson's $r = 0.92$). Support for both variables in univariable

models was similar ($\Delta AIC_c = 4.00$), but we considered the two-level factor variable to be simpler for interpretation.

Microsite characteristics considered in our survivorship models included soil VWC, soil depth, percentage cover of bare soil, litter/debris, and vegetation, and average heights of juveniles and overstory trees. We also accounted for the potential effects of seedling size (reviewed in Grossnickle 2018) by including seedling height and DRC samples (at time of planting) in our set of potential predictors. Interactions were considered for our openness variable and CWD treatment, openness and soil VWC (e.g. Gray et al. 2002; Davis et al. 2019), and height and DRC (Grossnickle 2005b). To reduce potential complexity in specifying a full (global) model for the basis of model selection, we first attempted dimension reduction. We accomplished this by evaluating the support of each individual variable relative to within-group support of other similar variables by comparing models of all possible variable combinations within a group (see next paragraph for further group details). All model specifications for this process included the base structure of openness, CWD treatment, and the Plot random effect. Favoring parsimony, we selected models from each group that had substantial support above other models ($\Delta AIC_c < 6.00$) in the group and above our base terms model. We used the resulting set of predictors to subsequently specify our global model.

In this group filtering, or dimension reduction process, we grouped soil VWC and depth, ground cover measurements, average heights of juveniles and overstory trees, and seedling height and DRC with their corresponding interactions (as considered above). We grouped variables this way to determine the potential contributions of these microsite characteristics, first within similar groups of variables (i.e. soils, ground cover, other tree vegetation, and seedling size), beyond our base treatment (canopy cover and CWD shelter) considerations. We expected

some of these groups or individual variables to contribute significantly to understanding variation in observed survivorship, but considered that not all measured characteristics of similar influences (for example, seedling height and DRC, or vegetation versus bare soil ground cover) would add substantial support over single variables. Our ground cover measurements began with the highest number of individual potential predictor variables, and so represented the greatest obstacle to meaningful dimension reduction. We first chose to sum percentage cover of all sampled vegetation, as distributions of survivors and non-survivors for both species experienced the same direction of effect by all (quadrat-) sampled vegetation life-forms (i.e. survivors were associated with less percentage cover of each vegetation type). However, the resulting summed vegetation variable, and other ground cover variables of bare soil, and litter/debris cover all had similar univariable support in within-group model comparisons. To further reduce complexity of this group of variables and leverage the relatively strong within-group correlations (Pearson's $|r| > 0.5$), we performed principal components analysis to establish no more than two axes accounting for the group variation to be used in final model specification and selection. Finally, we evaluated multicollinearity among predictor variables selected for final model development for each species as a result of this group filtering (dimension reduction) process, though no high correlations (Pearson's $|r| > 0.7$) were detected.

To develop a final model for each species, we first specified the full model with variables retained from the within-in group comparisons and filtering process. We expected microsite characteristics other than our base (canopy cover and CWD) treatment variables to account for some variation in survivorship of both species, but considered that the effects of some characteristics may change or become irrelevant with the effects of other characteristics accounted for. That is, it was not known prior to model development which combination of our

microsite variables would account for variance in our data, and it would be reasonable to assume that certain variable groups may be more or less important in a model conditional on the presence of others. Therefore, our final model selection process considered all possible combinations of variable groups (which in some cases were individual variables from a group, described above) in addition to base treatment terms as equally valid final candidate models. As with preceding steps, we ranked candidate models with AIC_c. However, in choosing a single final model for facilitating interpretation, models with similar support ($\Delta AIC_c < 6.00$) were further evaluated for their classification performance since we sought a final model with high discriminatory power for distinguishing survivors and non-survivors for each species. In these instances, we constructed confusion matrices from observations and predicted probabilities using a general threshold of 0.5 for distinguishing predicted successes, and compared classification metrics emphasizing success rates (since survival rates were low, dominating the total sample size). Specifically, we favored sensitivity (ratio of true positive predictions to all actual positives) and positive predictive value (PPV; ratio of true positive predictions to all positive predictions, akin to 1 minus the false positive rate). We also examined 95% confidence intervals of individual model estimates to determine reliability (whether confidence intervals included zero), and thus usefulness of individual terms in a given model. While we sought parsimony, our final candidate models with similar support differed by only one-two terms, so we also weighed the ecological benefit of additional information leading to better model discrimination ability.

Model fit of our final selected models included the preceding assessment of classification metrics as well as computing area under the curve (AUC) of a receiver operating characteristic (ROC) curve (Fawcett 2006) for the model (*pROC* package, Robin et al. 2011). AUC is commonly used as a measure of model fit for the discriminatory power of a model as assessed

across all possible thresholds distinguishing the probability of a successful event (here, survival). Plotted as a relationship between true-positive (sensitivity) and false-positive prediction rates, AUC is maximized with high sensitivity and PPV, and is no better than random guessing at values near 0.50. AUC ultimately indicates the probability that a randomly chosen positive and negative observation will classified correctly. Individual model term estimates were examined for strength of support, or significance, with 95% confidence intervals. Where confidence intervals overlapped zero, estimates were considered unreliable, or insignificant. Finally, we examined the relative strength of effect for each model term, or more specifically the relative importance of the variation in observed values for one variable than another in explaining survival, by comparing model coefficient estimates. Since the data were standardized and centered prior to model development, no additional standardization was necessary. To aid interpretation of effects of final model terms (i.e. evaluating effects on survival across the range of observed values for each term while holding other term constant), we evaluated partial effects of each term while holding others constant at their mean values using the *effects* package (Fox and Weisberg 2018).

1.2.4.2 Growth: Root Biomass

We attempted to analyze total root biomass in all surviving seedlings to determine any treatment effects on growth performance of each species, which should be indicative of seedlings establishing in the outplanting environment. New accumulation of root biomass was considered most important for seedling establishment in the first season after planting (e.g., Davis and Jacobs 2005), but aboveground biomass was not expected to differ meaningfully after one season, particularly in drought conditions (Grossnickle and MacDonald 2018). Additionally,

relating aboveground to belowground plant mass ratios may be meaningful in explaining establishment success (Grossnickle 2005a; Grossnickle 2018), but seedlings in this experiment were grown to the same development (e.g. target height, container size) specifications and so would not be expected to differ significantly in these ratios. Therefore, only root biomass data were analyzed for differences across treatments as a measure of seedling performance among survivors. The root biomass data were non-normal with non-constant variance and attempts at transformation were unsuccessful at resolving these issues. Therefore, we used nonparametric permutation tests (*perm* package in R, Fay and Shaw 2010) to examine the potential for differences in root biomass being attributable to silvicultural treatments. Specifically, for each species we tested for root biomass differences among all three canopy environments, and tested differences between each environment using a generalization of the permutation test for multiple comparisons (*rcompanion* package in R, Mangiafico 2019). Also, we tested for root biomass differences between our CWD shelter treatments (sheltered or not sheltered). Significance was set at a threshold of $\alpha = 0.05$.

1.3 Results

1.3.1 Canopy Treatment Environments, CWD, and Other Microsite Variables

The three canopy, or overstory environments in which we sampled, showed expected patterns of canopy cover differences, all of which were significant, in overstory basal area (m^2 ha^{-1}) and openness (% of sky) measurements (Table 1). Average density of overstory trees in non-harvested environments (continuous canopy cover) was significantly higher than in both harvested environments on average (25.12 m^2 ha^{-1} ±1.29 standard error; $P \leq 0.01$ for both pairwise comparisons), and comparatively low in variability about the mean, with a range of 0 to

Table 1. Summary characteristics (mean ± SE) for microsite variables considered for survival models of both species. Bolded and italicized figures indicate a significant difference across canopy environments for each reported microsite variable; corresponding superscripted letters indicate associated pairwise differences between canopy environments for each reported microsite variable, where environments sharing the same letter are not significantly different.

Canopy Environment	Plots	Basal Area (m^2 ha^{-1})	Openness (% of sky)	CWD (cm)	Mean Overstory Height (m)	Soil VWC (%)	Soil Depth (cm)	Bare Soil (%)	Litter/ Debris (%)	Vege-tation* (%)	Mean Juvenile Height** (m)	Juvenile Count**
No harvest	69	***25.12 (± 1.29)^a***	***28.56 (± 0.94)^a***	16.51 (± 0.57)	***16.09 (± 0.53)^a***	***10.85 (± 0.44)^a***	17.56 (± 0.39)	10.22 (± 2.19)	61.52 (± 2.97)	***47.61 (± 3.46)^a***	***4.99 (± 0.46)^a***	***23.73 (± 1.76)^a***
Group-selection	69	***4.13 (± 0.55)^b***	***62.90 (± 1.11)^b***	15.40 (± 0.45)	***9.00 (± 1.01)^b***	***15.24 (± 1.07)^b***	17.01 (± 0.48)	9.42 (± 1.89)	66.09 (± 2.78)	***36.59 (± 3.32)^b***	***2.96 (± 0.43)^b***	***12.22 (± 2.02)^b***
Individual-tree selection	68	***14.45 (± 1.04)^c***	***49.89 (± 1.01)^c***	16.32 (± 0.67)	***17.45 (± 0.69)^a***	***13.64 (± 0.97)^b***	16.76 (± 0.46)	9.34 (± 1.86)	71.03 (± 2.85)	***36.99 (± 3.26)^b***	***2.40 (± 0.32)^b***	***8.84 (± 1.38)^b***

** Vegetation is a summation of cover measurements for graminoid, forb, shrub, and moss life-forms.*

*** Sample sizes for these measurements were 60 for no harvest, 69 for group-selection, and 57 for individual-tree selection overstory types.*

50.5 m^2 ha^{-1}. Correspondingly, openness in these non-harvested areas was the lowest among the three overstory environments (28.56% ±0.94; $P \leq 0.01$ for both pairwise comparisons), though the most variable of the three environments in this measure. Group-selection openings had the least overstory density on average across the three treatments (4.13 m^2 ha^{-1} ±0.55; $P \leq 0.01$ for both pairwise comparisons), but showed the most variation on average about the mean, likely due to differences between opening interiors (lower to zero density) and edges (0 to 16.07 m^2 ha^{-1} range). Openness in group-selection openings was, on average, higher and less variable about the mean than the other overstory environments (62.90% ±1.11; $P \leq 0.01$ for both pairwise comparisons). By basal area measurements, average overstory density in our individual-tree selection treatment area fell roughly halfway (14.45 m^2 ha^{-1} ±1.05; $P \leq 0.01$ for both pairwise comparisons; 0 to 36.73 m^2 ha^{-1} range) between non-harvested and group-selection treatments. Openness in the individual-tree selection treatment area was also intermediate relative to other treatments (49.89% ±1.01; $P \leq 0.01$ for both pairwise comparisons), but more similar to group-selection than non-harvested areas, presumably from differences in average tree size between harvest and non-harvest areas (see preceding qualitative description note in *Methods: Experimental Design*).

Size of CWD (mean height from ground to top of debris) chosen for shelter effects at each plot was similar on average and not significantly different across overstory environments (Table 1), supporting our subsequent analysis of this effect as a two-level factor rather than continuous predictor. Average size in non-harvested areas was 16.51 cm (±0.57; $P = 0.38$ for group-selection comparison; $P = 0.83$ for individual-tree selection comparison), 16.32 cm in individual-tree selection treatments (±0.67; $P = 0.38$ for group-selection comparison; $P = 0.83$ for no harvest comparison), and 15.40 cm in group-selection treatments (±0.49; $P = 0.38$ for both

pairwise comparisons). Notably, mean size across overstory treatment areas was greater than twice our minimum size criterion (7.6 cm), which was based on sufficiency for sheltering tree seedlings at a minimum target height of 10.2 cm (see *Methods*). However, our average seedling height across species was 15.8 cm (±0.23), also well above the minimum target height. Nonetheless, on average, inclusive of both species, our CWD size was still greater in proportion to average tree size (spruce 18.95 cm ±0.15, pine 12.62 cm ±0.18) than our design required, ensuring that seedlings planted with CWD shelter were in fact sufficiently sheltered on average.

Mean height of sampled overstory trees was significantly higher in individual-tree selection treatments (17.45 m ±0.69) as compared with group-selection treatments (9.00 m ±1.01; $P \leq 0.01$ for pairwise comparison), but not significantly different from that in non-harvested environments (16.09 m ±0.53; $P \leq 0.12$ for pairwise comparison) (Table 1). Mean overstory height was comparatively small and variable in group-selection treatments (9.00 m ±1.01) since sampled overstory trees were a mix of advance regeneration and mature canopy trees at opening edges, and significantly different from other canopy environments ($P \leq 0.01$ for both pairwise comparisons). Our samples of regeneration (with a reduced sample size of 186 total plots) showed significantly greater numbers of juvenile trees and average height of juveniles on average in non-harvested environments (height 4.99 m ±0.46, count 23.73 ±1.76) as compared to both harvest environments (non-harvested environments ($P \leq 0.01$ for pairwise comparison). In group-selection treatment areas, average counts (12.22 ±2.02) were similar to those in individual-tree selection treatment areas (8.84 ±1.38; $P \leq 0.17$ for pairwise comparison), as were mean heights on average (2.96 m ±0.43 and 2.40 ±0.32, respectively; $P \leq 0.29$ for pairwise comparison).

Results from our soil core samples at each plot showed that volume of water per volume of soil (soil volumetric water content, soil VWC) sampled increased with openness of the overstory environment (or, inversely with overstory tree density), but that average depth to restriction of soils was similar across overstory environments (Table 1). Across environments, soil moisture was highly variable, as low as zero percent to nearly 50% of the soil volume sampled. Minimum values of sampled soil moisture were lowest in individual-tree selection treatments (0.00%), followed by non-harvested areas (2.12%) and group-selection treatments (3.50%). Maximum sampled soil moisture followed the same pattern as mean values across environments, significantly lower and least variable in non-harvested (max 23.47%; mean 10.85% ±0.44; $P \leq 0.01$ for both pairwise comparisons) and significantly higher in group-selection openings (max 48.70%; mean 15.24% ±1.07) and the individual-tree selection environment (max 35.33%; mean 13.64% ±0.97), with no significant difference between the two harvest environments ($P = 0.27$ for pairwise comparison). Variability was similar in the latter two environments. In contrast, our target soil depth of 20 cm was reached in all environments, and minimums were near 7.5 cm for non-harvested and individual-tree selection areas, and only 3.1 cm in one instance of group-selection areas. Mean soil depth was near 17 cm in each environment and not significantly different ($P = 0.19$-0.70 for pairwise comparisons), with similar variability (17.56 cm ±0.39, 17.01 cm ±0.48, 16.76 cm ±0.46 in non-harvested, group-selection, and individual-tree selection treatments, respectively).

Similar patterns of separation across overstory environments were not as evident in our microsite measurements for percentage cover of bare soil, litter/debris, and vegetation (including forb, shrub, graminoid, and moss life-forms) (Table 1). The occurrence of bare mineral soil across environments was low relative to total quadrat area, with over 50% of plots containing no

bare soil. No differences between each environment were significantly different (P = 0.76-0.98 for pairwise comparisons) and observed values were highly variable for each environment (10.22% ±2.19 in non-harvested, 9.42% ±1.89 in group-selection, and 9.34% ±1.86 in individual-tree selection canopy environments). In contrast, litter and debris coverage, including all dead herbaceous and woody material not incorporated into the soil, was consistently high with relatively low variability across all environments. Greater cover of litter and debris in silvicultural regeneration treatment areas (66.09% ±2.78 for group-selection; 71.03% ±2.85 for individual-tree selection) compared to non-harvested areas (61.52% ±2.97) was likely due to additional debris resulting from harvest activities compared to the non-harvest environments, but no pairwise differences were significant (P = 0.07-0.26 for pairwise comparisons). In this study, the presence of litter and debris often occurred with vegetation, but qualitative observations suggested larger pieces of litter and debris in post-harvest environments excluded vegetation on average more than in non-harvest areas. We found this rough trend in our data, with significant differences between non-harvested (47.61% ±3.46) and both harvested (36.99% ±3.26 and 36.59% ±3.32 for individual-tree selection and group-selection treatments, respectively) canopy environment pairwise comparisons (P = 0.04 for both pairwise comparisons), but no difference between harvested environments, group-selection and individual-tree selection treatments (P = 0.93 for pairwise comparison).

1.3.2 Engelmann Spruce Survival

Survival of individual spruce seedlings was low across all treatments on average (77 of 412 total individuals), with a considerable amount of variability (18.69% ±1.92). Spruce survival was highest in the individual-tree selection treatment (26.50% ±3.80) and significantly

different ($P \leq 0.01$ for pairwise comparison) from the lowest survival which occurred in the non-harvest treatment (8.70% ±2.41). Survival was not significantly different between individual-tree selection and group-selection treatments ($P = 0.29$ for pairwise comparison; Figure 5). Along our continuous measure of canopy cover (% openness), mean survival occurred at approximately 52% (±1.75) openness, whereas non-survivors occurred on average at a cover of just under 46% (±0.91), a difference which was significantly different ($P \leq 0.01$). Survival with CWD shelter was significantly greater ($P \leq 0.01$) at over 200% of the survival without CWD shelter (25.20% ±3.03 and 12.10% ±2.28, respectively) across overstory environments, with greater variability in survival without CWD shelter.

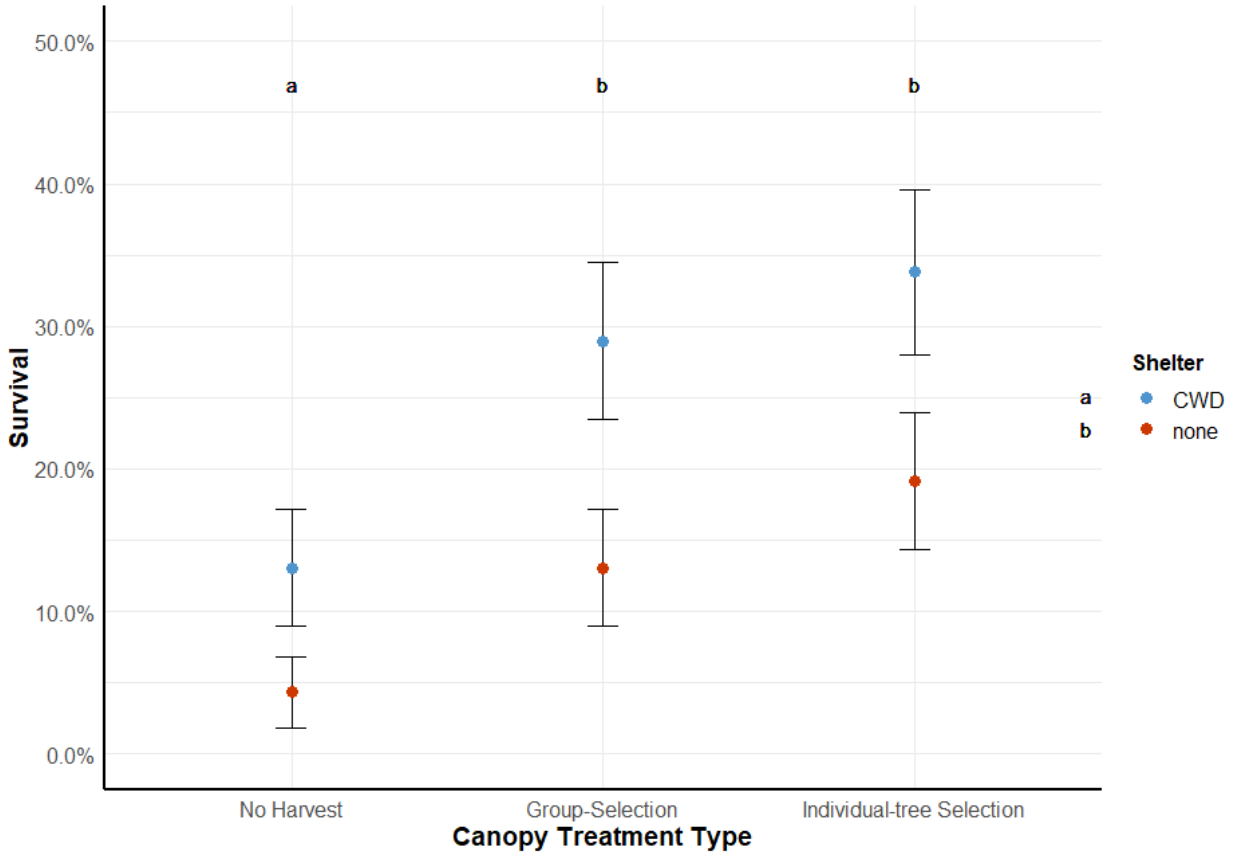

Figure 5. Percent of surviving spruce seedlings relative to total planted spruce by canopy environment (harvest or silvicultural regeneration treatment type, or none) and coarse woody debris shelter (or none). Vertical bars from each point indicate standard error of the observed mean survival for each treatment. Coarse woody debris-sheltered

seedlings are indicated by blue points, and non-sheltered seedlings are indicated by red points. Significant differences between canopy environments are indicated by bolded lowercase letters at the top of the figure; environments sharing the same letter do not differ significantly in mean survival. Similarly, significant differences between coarse woody debris treatments are indicated by bolded lowercase letters at the right side of the figure corresponding to the treatment legend (color).

Our full logistic model for spruce survivorship, after dimension reduction and filtering among potential predictor variables, included estimates for the fixed-effects of base terms (openness and CWD shelter), seedling height, soil moisture, soil depth, the first principal component axis for ground cover data, and average height of surrounding juvenile trees. Subsequent evaluation of candidates for alternative final models resulted in three models in addition to the full model with similar support ($\Delta AIC_c < 6.00$) (Table 2). Two models (full and one alternative) included an unreliable estimate for the effect of average juvenile tree height on survival, and so were dropped from consideration. The two remaining models in consideration differed by only the inclusion of our first ground cover principal component. The comparison of classification metrics between the two models, at a threshold of 0.5, was only a difference of two predictions of survival for observed non-survivors in the model including the additional term. While sensitivity was identical for the two models (52.86%), the slight difference in specificity (true non-survival) meant a difference of four percentage points for the PPV (86.05% vs. 90.24%). Due to this difference in classification and added simplicity of less terms, we selected the candidate model without the ground cover variable as our final model of spruce survival ("Alt3" in Table 2).

Since our final selected model did not contain the juvenile tree height term, for which less data were available (juveniles not sampled at all plots; see *Results* microsite variables summary), we refit our final model to the full dataset (412 observations) prior to further evaluating fit and interpreting effects. In the final refit model, the effect of overstory openness on spruce survival

Table 2. Details for final spruce survival model candidates (full and alternates) with similar support ($\Delta AIC_c < 6.00$), including coefficient estimates, model log-likelihood (LL), and classification metrics. Covariates include canopy openness (%), coarse woody debris shelter treatment (model estimate for effect of no shelter, or "none"), seedling height at planting ("Height"), soil moisture ("Soil VWC"), soil depth, and principal component axis 1 for ground cover variables (litter/debris, vegetation, and bare soil)*. Classification metrics include sensitivity (% of predicted survival relative to observed survival; 0.5 probability threshold), positive predictive value (% of correctly predicted survival relative to all predicted survivors; 0.5 probability threshold), and area under the receiver operating curve (AUC; correct classification rate over all possible thresholds). Significant model estimates (confidence intervals not including zero) are indicated by bold and italicized font. Variables not present in a model are indicated with *NA* estimate values. Our final selected model ("Alt3") is indicated by a dashed border.

Model	Openness (%)	CWD (none)	Height (cm)	Soil VWC (%)	Soil Depth (cm)	Ground Cover PC1*	Juvenile Height (m)	LL	AIC_c	ΔAIC_c	Sensitivity (%)	PPV (%)	AUC
Full	0.185	***-1.569***	***-0.914***	***0.739***	***0.682***	***-0.344***	-0.378	-137.50	293.50	0.00	50.00	85.37	0.94
Alt1	0.300	***-1.579***	***-0.924***	***0.777***	***0.700***	***-0.371***	*NA*	-138.86	294.10	0.62	52.86	86.05	0.94
Alt2	0.198	***-1.584***	***-0.906***	***0.886***	***0.732***	*NA*	-0.431	-139.58	295.60	2.06	50.00	87.50	0.94
Alt3	0.336	***-1.599***	***-0.916***	***0.947***	***0.760***	*NA*	*NA*	-141.24	296.80	3.28	52.86	90.24	0.95

***** Principal component axis 1 representing (Pearson's correlations) a strong negative relationship with litter/debris ($r = -0.98$), and positive relationships with vegetation ($r = 0.68$) and soil ($r = 0.55$).

was slightly positive (β_{Open} = 0.3976 ±0.2402), the relationship with non-CWD shelter was very strongly negative (β_{CWD} = -1.5688 ±0.4329), the effect of seedling height was strongly negative (β_{Ht} = -0.9435 ±0.3263), and the effects of soil VWC and depth were strong and positive (β_{SVWC} = 1.0600 ±0.2849 and β_{SDepth} = 0.5784 ±0.2484). All estimates were significant, except for the openness estimate, where the 95% confidence interval for which was large and included zero (-0.0574 to 0.9696). Since data were standardized to mean zero and standard deviation of one prior to modeling, estimate sizes are directly comparable (Figure 6). As such, the relative magnitude of each variable on survivorship, from highest to lowest, was CWD shelter, soil VWC, height, soil depth, and openness.

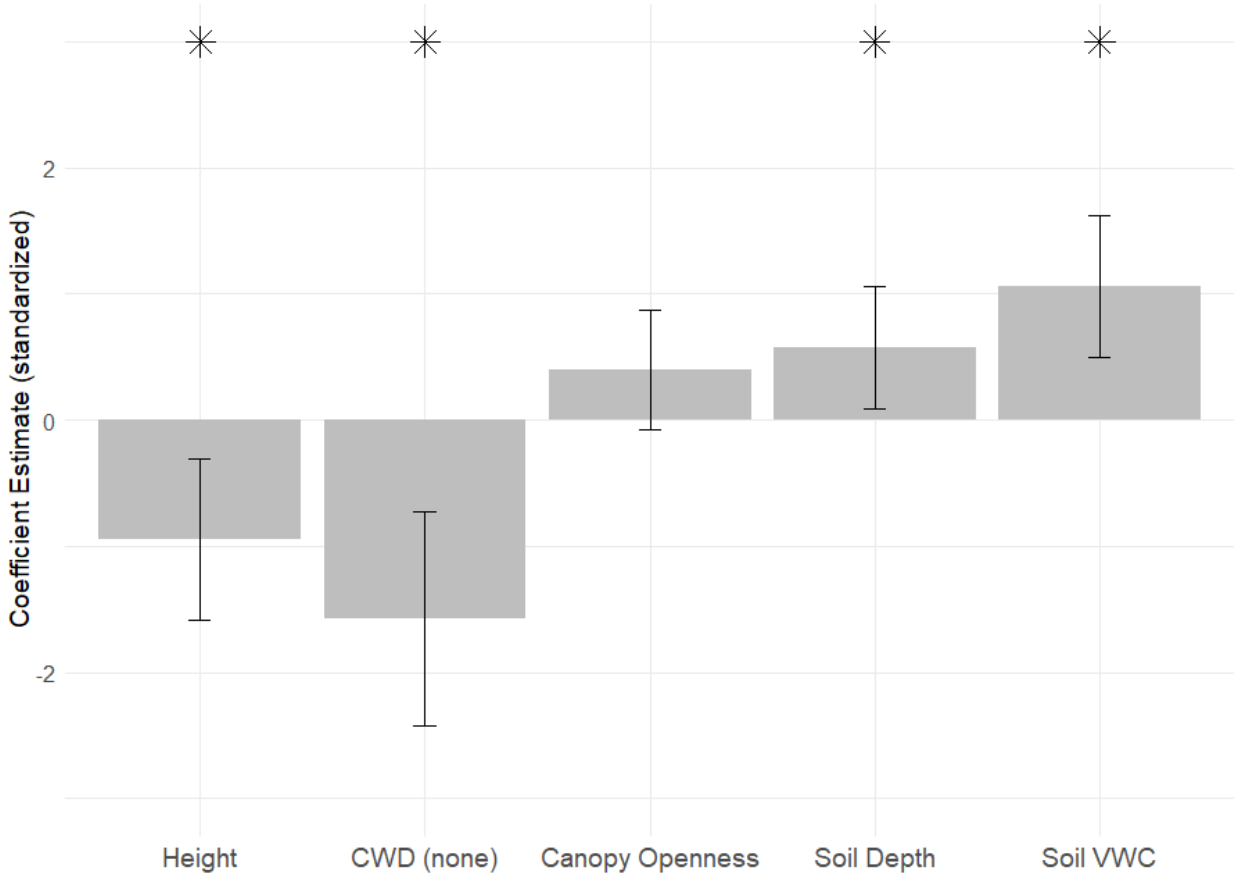

Figure 6. Final selected spruce survival model coefficient estimates relative magnitude (standardized effects) and direction. Covariates include seedling height at planting ("Height"), coarse woody debris shelter treatment (model

estimate for effect of no shelter, or "none"), canopy openness (%), soil depth, and soil moisture ("Soil VWC"). Vertical lines indicate 95% confidence intervals. Asterisks indicate significant effects, based on reliability of estimates given confidence intervals including zero.

The model fit to our data as assessed by AUC was exceptional (AUC = 0.971 ±0.015), indicating that the model was able to discriminate well between spruce survivors and non-survivors. From a confusion matrix constructed at a probability of success threshold of 0.5, only 4 observed non-survivors were classified incorrectly (98.81% specificity), while 41 of 77 (53.25%) of observed survivors were classified successfully (sensitivity), resulting in a PPV of 91.11%. Overall accuracy was 90.29% (95% confidence interval of 87.01% to 92.97%). Predicted survival probabilities were mostly very low (mean 0.16 ±0.01, median 0.06), but were as high as 0.97. Following the relative effects from our final model predictors, the influence on predicted survival probabilities was strongest for CWD shelter treatments, nearly 4.5 times higher (but also more variable) for sheltered versus unsheltered seedlings on average (Figure 7). Over the observed range of soil VWC percentages, predicted probability of survival increased most sharply above the mean observed moisture content, which was 13.24%. Predicted probabilities beyond a one standard deviation change (7.40 %) in soil VWC, to which the model coefficient applies, showed high uncertainty. Seedling height at planting also strongly influenced survival probability in our model, suggesting at least 150% change in survival probability with a one standard deviation (3.14 cm) decrease in height from the mean (18.95 cm) observed height. Changes in predicted probabilities of survival with canopy openness and soil depth influences were comparatively minimal, but less variable overall. For both variables, the observed data was variable (47.10% mean canopy openness with standard deviation 16.53%; 17.11 cm mean soil depth with standard deviation 3.67 cm), but survival probability predictions almost never exceeded 0.10 across the range of observed values.

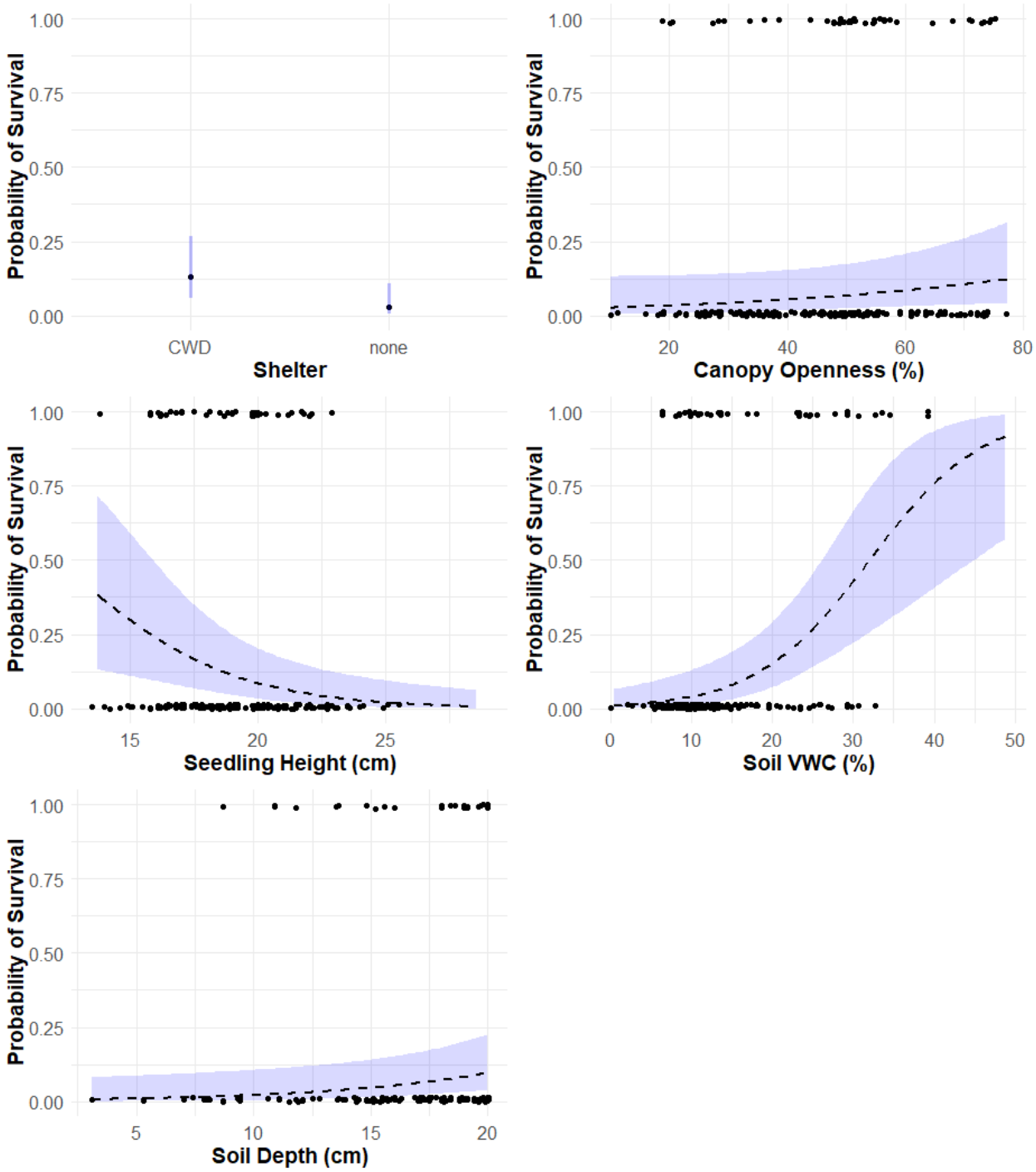

Figure 7. Predicted mean effects of microsite variables in the final selected spruce survival model. Covariates include coarse woody debris shelter treatment (shelter by "CWD" or no shelter), canopy cover (% canopy openness), seedling height at planting, percent soil moisture, and soil depth. Predictions were made across observed values of each variable. Predicted survival across levels of each variable is indicated by the dashed line (points for shelter factor effects), and colored bands (bars on shelter factor effects) on either side of the line show smoothed 95% confidence intervals for predicted mean survival. Black points in each panel (except the coarse woody debris effect panel) indicate distribution of observed survivors and non-survivors across the observed values of each variable. All effects except that of canopy openness were significant (Figure 6).

1.3.3 Ponderosa Pine Survival

Survival of individual pine seedlings (Figure 8) was greater than spruce but still low across all treatments on average (143 of 412 total individuals), with a relatively moderate variability (34.71% ±2.35). Pine survival was similar in across canopy treatment environments, with no significant differences between pairwise comparisons (P = 0.40-0.83 for pairwise comparisons). Pine survival in the individual-tree selection treatment was 36.80% (±4.15), slightly more than in the non-harvest treatment (35.50% ±4.09) and the group-selection treatment (31.90% ±3.98). Along our continuous measure of canopy cover (% openness), mean pine survival occurred at a cover of approximately 46% (±1.43), whereas non-survivors occurred on average at a cover of just under 48% (±0.99), though this difference was not significant (P = 0.32). Survival with CWD shelter was significantly higher ($P \leq 0.01$) and 198% of the survival without CWD shelter (46.10% ±3.48 and 23.30% ±2.95, respectively) across overstory environments, with more variation for those without CWD shelter.

The full model fit to our pine survivorship data included estimates for the fixed-effects of base terms (openness and CWD shelter), seedling height, soil VWC, the first principal component axis for ground cover data, and average height of juvenile trees. In addition to the full model, two other evaluated models showed similar support ($\Delta AIC_c < 6.00$) (Table 3). Of these two alternative models, one differed from the full model in the absence of average juvenile tree height variable ("Alt1," Table 3), and another in the absence of the ground cover variable ("Alt2," Table 3). Furthermore, the model excluding average juvenile tree heights had an unreliable estimate for the openness predictor, but we did not exclude the model from consideration for this reason since the variable would be present in any final model, given our *a priori* decision, regardless of reliability. Thus, the three candidates were assessed on

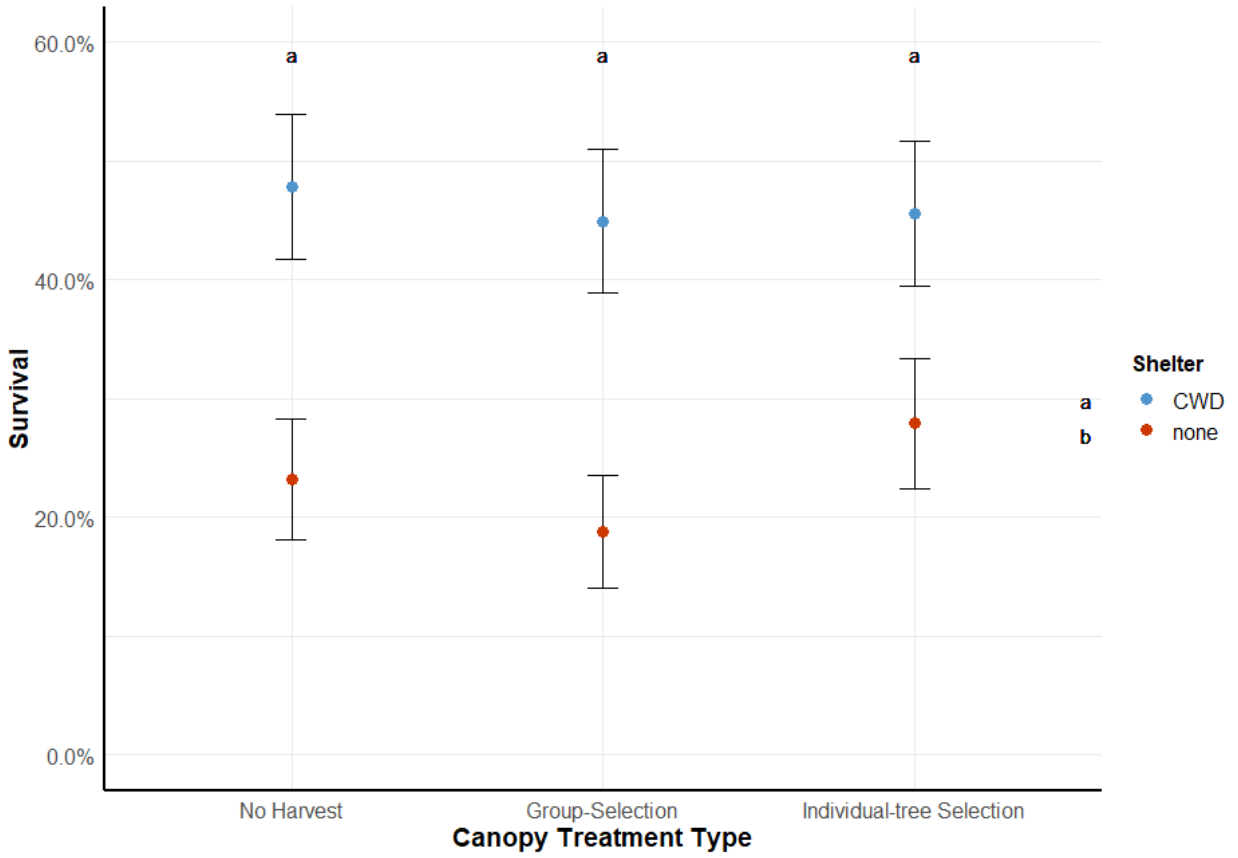

Figure 8. Percent of surviving pine seedlings relative to total planted pine by canopy environment (harvest or silvicultural regeneration treatment type, or none) and coarse woody debris shelter (or none). Vertical bars from each point indicate standard error of the observed mean survival for each treatment. Coarse woody debris-sheltered seedlings are indicated by blue points, and non-sheltered seedlings are indicated by red points. Significant differences between canopy environments are indicated by bolded lowercase letters at the top of the figure; environments sharing the same letter do not differ significantly in mean survival. Similarly, significant differences between coarse woody debris treatments is indicated by bolded lowercase letters at the right side of the figure corresponding to the treatment legend (color).

classification metrics comparisons. Given a classification threshold of 0.5, full model sensitivity (50.39%) was higher than alternatives (47.24% and 48.03%). However, full model PPV was lower (77.11%) than the alternative excluding the ground cover variable (81.33%), but higher than the second alternative (75.00%). Due to the added parsimony of the alternative excluding the ground cover variable over the full model, similar sensitivity, better PPV, and better overall accuracy (better in all metrics over the second alternative), we chose this alternative as our final model ("Alt2," Table 3). Since this model included the average juvenile height variable, we did

Table 3. Details for final pine survival model candidates (full and alternates) with similar support (ΔAICc < 6.00), including coefficient estimates, model log-likelihood (LL), and classification metrics. Covariates include canopy openness (%), coarse woody debris shelter treatment (model estimate for effect of no shelter, or "none"), seedling height at planting ("Height"), soil moisture ("Soil VWC"), principal component axis 1 ("PC1") for ground cover variables (litter/debris, vegetation, and bare soil)*, and mean height of surrounding (natural regeneration) juvenile trees. Classification metrics include sensitivity (% of predicted survival relative to observed survival; 0.5 probability threshold), positive predictive value (% of correctly predicted survival relative to all predicted survivors; 0.5 probability threshold), and area under the receiver operating curve (AUC; correct classification rate over all possible thresholds). Significant model estimates (confidence intervals not including zero) are indicated by bold and italicized font. Variables not present in a model are indicated with *NA* estimate values. Our final selected model ("Alt3") is indicated by a dashed border.

Model	Openness (%)	CWD (none)	Height (cm)	Soil VWC (%)	Ground Cover PC1*	Juvenile Height (m)	LL	AIC_c	ΔAIC_c	Sensitivity (%)	PPV (%)	AUC
Full	***-0.376***	***-1.326***	***-0.613***	***0.645***	***-0.253***	***-0.294***	-199.61	415.60	0.00	50.39	77.11	0.83
Alt1	-0.273	***-1.324***	***-0.634***	***0.645***	***-0.277***	*NA*	-201.64	417.60	1.97	47.24	75.00	0.83
Alt2	***-0.375***	***-1.324***	***-0.621***	***0.741***	*NA*	***-0.333***	-202.22	418.80	3.14	48.03	81.33	0.84

***** Principal component axis 1 representing (Pearson's correlations) a strong negative relationship with litter/debris (r = -0.98), and positive relationships with vegetation (r = 0.71) and soil (r = 0.52).

not refit the model as we were unable to use the full data set for missing plot samples of average juvenile height.

All effects of predictor variables on pine survivorship in our final selected logistic model (372 observations) were negative, except for a positive relationship with soil VWC (Table 3; Figure 9). More specifically, the effects of openness were relatively minimal and negative (β_{Open} = -0.3748 ±0.1557), survival was very strongly negatively related to the absence of CWD shelter (β_{CWD} = -1.3241 ±0.2838), effects of seedling height were moderate and negative (β_{Ht} = -0.6208 ±0.1876), soil VWC had a moderate positive effect (β_{SVWC} = 0.7405 ±0.1555), and the effects of average juvenile tree height were minimal and negative (β_{RHt} = -0.3333 ±0.1540). All coefficient estimates were reliable as no confidence intervals (95%) included zero. Having standardized the data to mean zero and standard deviation of one prior to model fitting, each estimate size is directly comparable for relative magnitude of effect (Figure 9). Therefore, the ordering of predictors according to relative magnitude of effect for pine survivorship was CWD shelter, soil VWC, seedling height, openness, and average juvenile tree height.

Calculation of AUC suggested good fit for our final selected pine survivorship model (AUC = 0.840 ±0.044), indicating good discrimination of survivors and non-survivors by our model. Given a confusion matrix constructed on a 0.5 probability of success threshold, only 14 observations of non-survival were misclassified by the model (94.29% specificity), but more observations of survival were misclassified than correctly classified (61 of 127 correct, 48.03% sensitivity). With relatively few false positives predicted by the model, PPV was 81.33%, while overall accuracy was 78.49% (95% confidence interval of 73.97% to 82.56%). Predicted probability of survival from our pine survival model was generally low (mean 0.33 ±0.01, median 0.29), but much higher than that of our spruce survival model. Similar to spruce, the

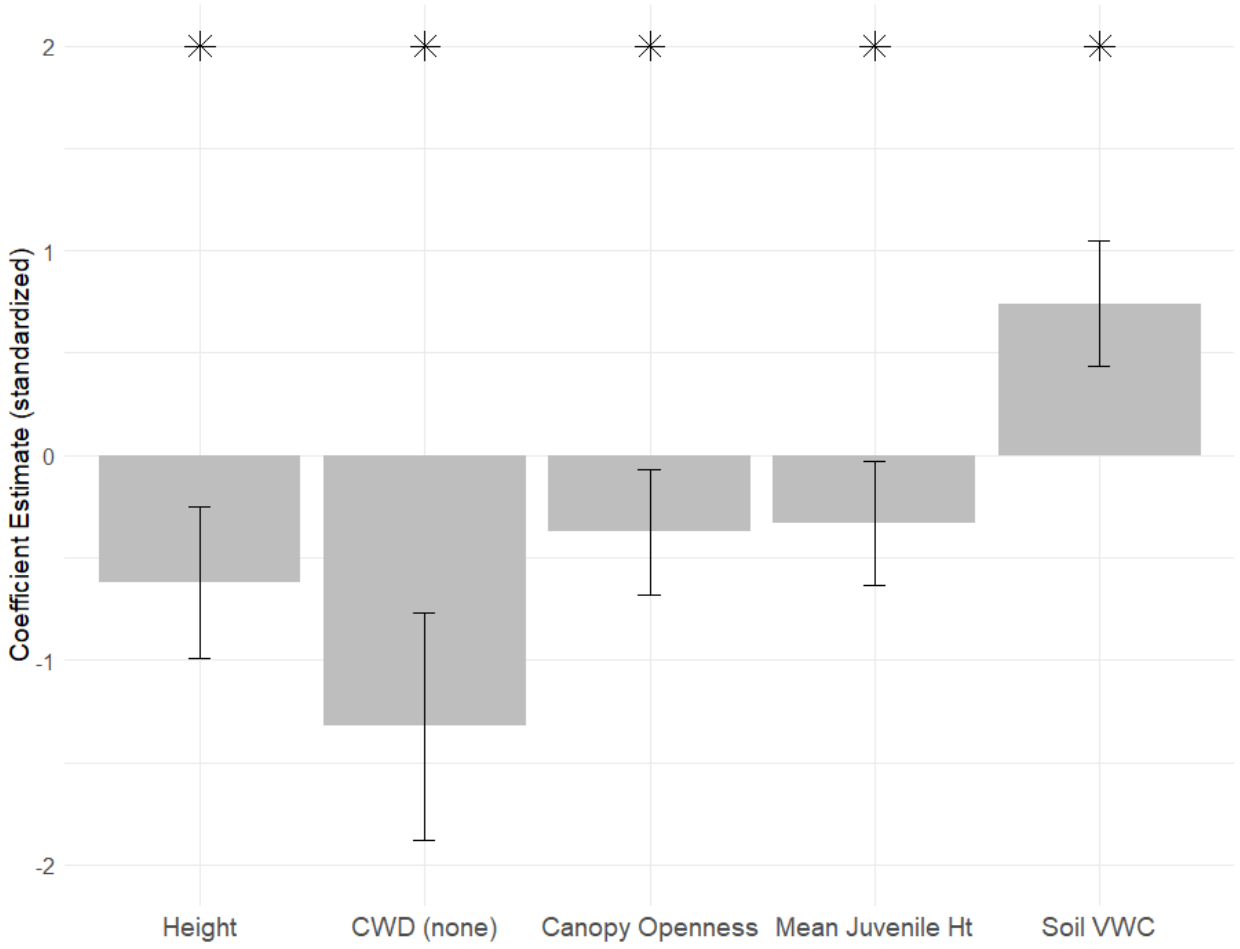

Figure 9. Final selected pine survival model coefficient estimate relative magnitude (standardized effects) and direction. Covariates include seedling height at planting ("Height"), coarse woody debris shelter treatment (model estimate for effect of no shelter, or "none"), canopy cover (percent canopy openness), mean height of surrounding juvenile trees (natural regeneration; "Mean Juvenile Ht"), and soil moisture ("Soil VWC"). Vertical lines indicate 95% confidence intervals. Asterisks indicate significant effects, based on reliability of estimates given confidence intervals including zero.

strongest relative influence on pine survival probability in our model resulted from CWD shelter treatments, which showed 2.5 times higher probability of survival in sheltered versus unsheltered treatments, though predictions were highly variable in both cases (Figure 10). Soil VWC had a strong influence on probability of survival for pine as well, resulting in a nearly 150% increase in survival probability with a one standard deviation (7.66%) increase from the observed mean (13.47%). For pine, the influence of seedling height at planting was a strong negative influence on survival, with a roughly 150% increase in survival probability given a one standard deviation

(3.58 cm) decrease from the mean observed height (12.70 cm). Influences of canopy openness and mean height of surrounding juvenile trees both had similarly relatively small influences on pine survival probability. For both predictors, one stand deviation decreases from mean observed values (47.99% mean canopy openness, stand deviation 16.49%; 3.45 m mean juvenile tree height, stand deviation 3.34 m) both resulted in differences in survival probability of only about 0.10.

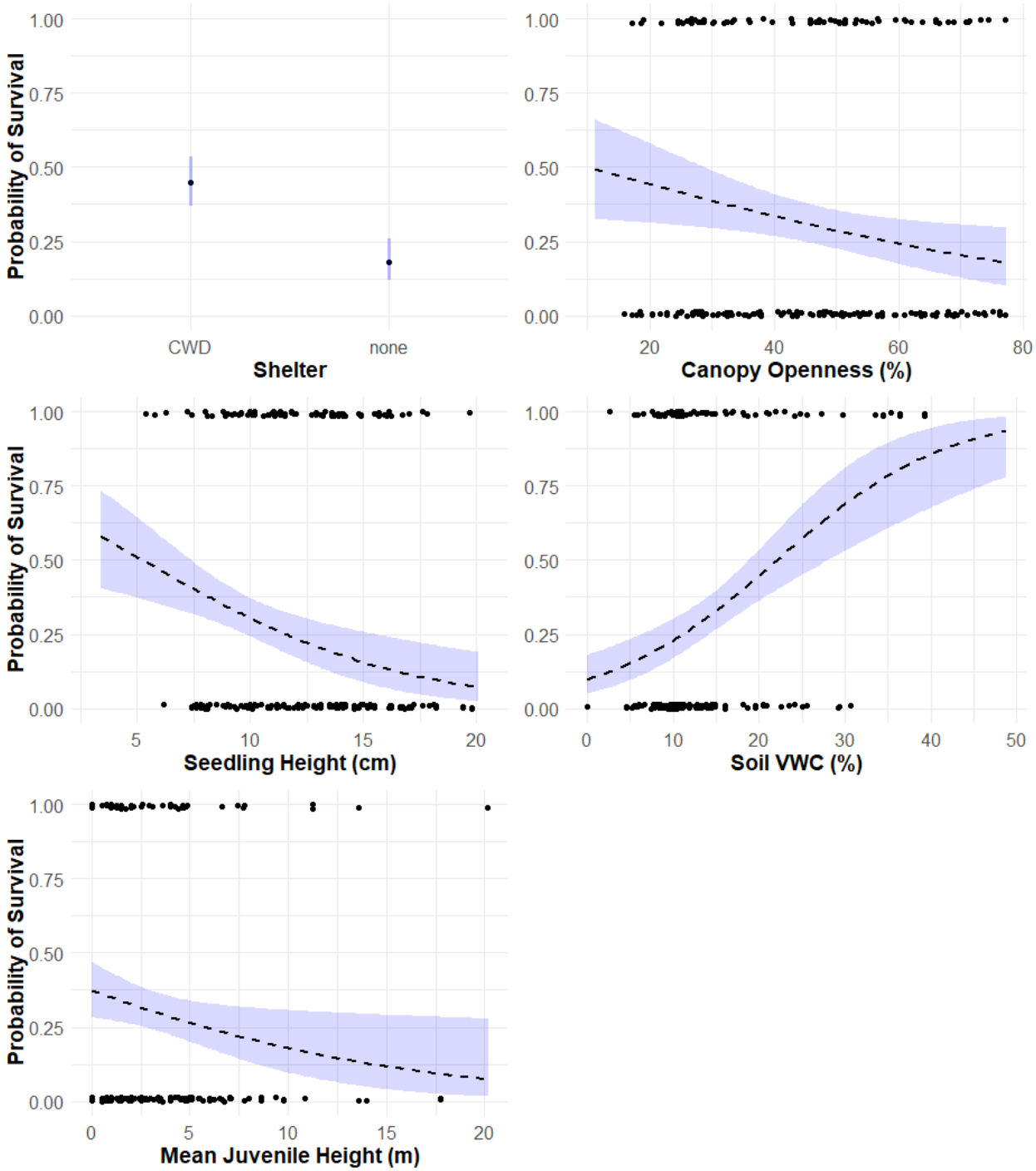

Figure 10. Predicted mean effects of microsite variables in the final selected pine survival model. Covariates include coarse woody debris shelter treatment (shelter by "CWD" or no shelter), canopy cover (% canopy openness), seedling height at planting, percent soil moisture ("Soil VWC"), and mean height of surrounding juvenile trees (natural regeneration). Predictions were made across observed values of each variable. Predicted survival across levels of each variable is indicated by the dashed line (points for CWD shelter factor effects), and colored bands (bars on CWD shelter factor effects) on either side of the line show smoothed 95% confidence intervals for predicted mean survival. Black points in each panel (except the coarse woody debris effect panel) indicate distribution of observed survivors and non-survivors across the observed values of each variable. All effects except that of canopy openness were significant (Figure 6).

1.3.4 Root Biomass

Root biomass values for spruce (0.67 g ±0.05) were much lower on average than for pine (0.94 g ±0.04), but minimum observed root biomass was the same in both species (0.20 g), and overall data were more strongly skewed for spruce than pine. Permutation tests for treatment effects on root biomass for both species showed significant differences between harvested and non-harvested canopy environments, and contrasting responses to CWD shelter treatments (Figure 11). Spruce root biomass for surviving seedlings was lower on average in the non-harvested canopy environment (0.31 g ±0.03) compared to group selection openings (0.70 g ±0.05) and individual-tree selection treatments (0.77 g ±0.08). These differences were significant ($P < 0.01$ for each) between non-harvested and both harvested treatments but were not significant ($P = 0.49$) between group-selection and individual-tree selection treatments. In CWD shelter treatments, spruce root biomass was nearly identical (0.67 g ±0.06) to non-sheltered seedlings (0.66 g ±0.08), a difference which was not significant ($P = 1.00$). Pine root biomass for surviving seedlings was also lower on average in non-harvested canopy areas (0.68 g ±0.04) compared to group selection openings (1.00 g ±0.07) and individual-tree selection harvest (1.12 g ±0.08). Between non-harvested and each harvest environment, these differences were significant ($P < 0.01$ in both cases), but not between harvest treatments ($P = 0.27$). Root biomass of pine seedlings showed greater difference than spruce between CWD shelter treatments (0.87 g ±0.05 for sheltered, 1.07 ±0.08), a difference which was significant ($P = 0.03$).

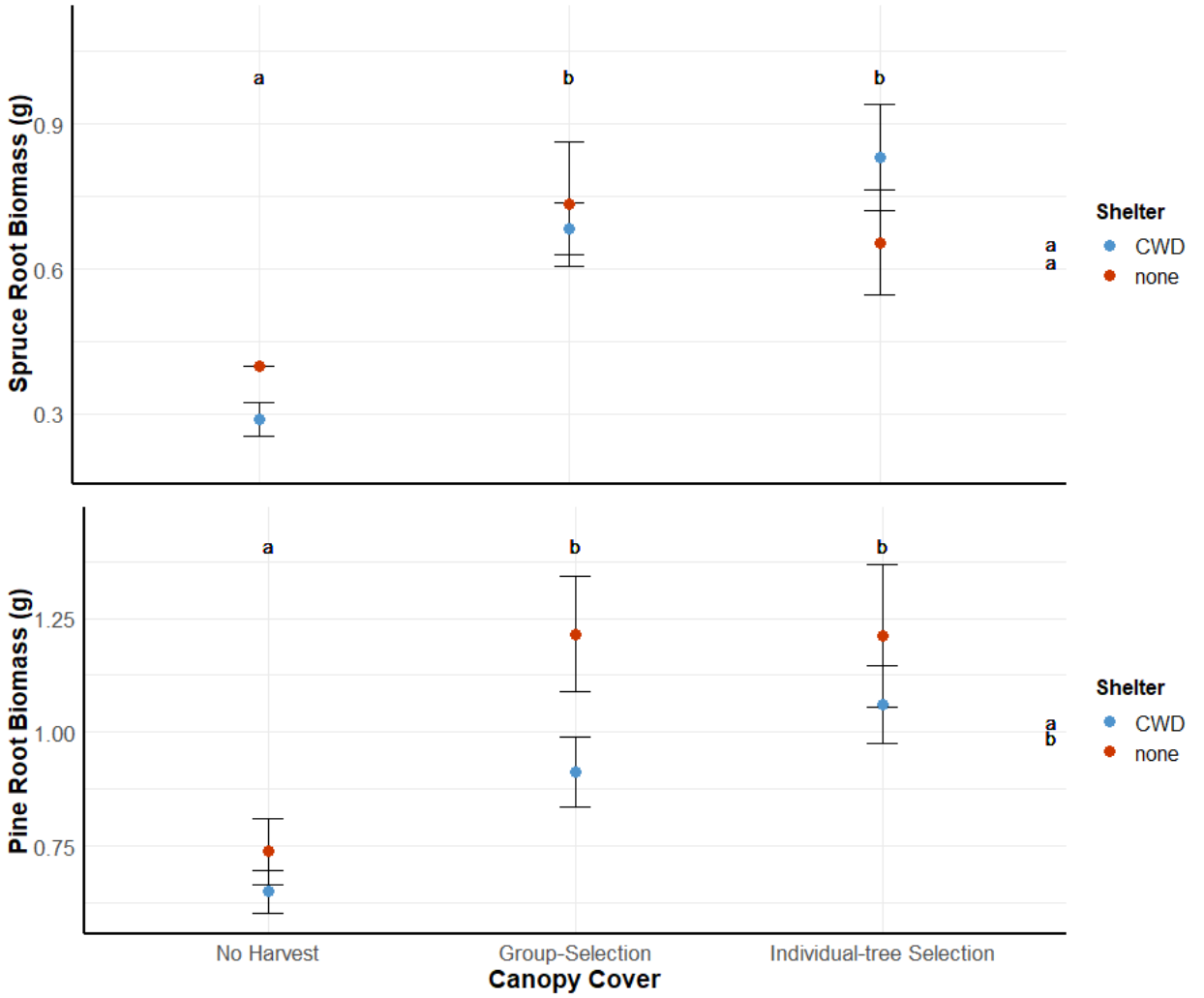

Figure 11. Root biomass for spruce (top panel) and pine (bottom panel) by canopy cover type (harvest or silvicultural regeneration treatment type, or none) and coarse woody debris shelter (or none). Vertical bars from each point indicate standard error of the observed proportion of survival for each treatment. Coarse woody debris-sheltered seedlings are indicated by blue points, and non-sheltered seedlings are indicated by red points. Note the difference in extent of scales of root biomass values for each species. Our permutation tests suggested that, for both species, differences in biomass were different between no harvest and harvested canopy types, but not between harvested environments nor between CWD shelter treatments. Significant differences between canopy environments are indicated by bolded lowercase letters at the top of the figure; environments sharing the same letter do not differ significantly in mean survival. Similarly, significant differences between coarse woody debris treatments are indicated by bolded lowercase letters at the right side of the figure corresponding to the treatment legend (color).

1.4 Discussion

Reforestation strategies and tactics are focal points in adaptive silviculture for responding to climate change (Spittlehouse 2005; Larson and Funk 2016; Nolan et al. 2018; North et al. 2019) and should carefully account for microsite influences on the regeneration environment which determine success, especially those resulting from silvicultural practices (Chmura et al. 2011; Anderson and Puettmann 2017). Because reforestation strategies in adaptive contexts may include managing for a diversity of species (e.g. Messier et al. 2016; Hof et al. 2017; Astrup et al. 2018; Guldin 2019), understanding the relative performance of different species under current management techniques will help to inform adaptive management alternatives in the future. In low-elevation Engelmann spruce forests of the central-southern Rocky Mountains, these considerations are amplified by expectations that viability of spruce populations will sharply decline with warming climate conditions (Rehfeldt et al. 2015; Conlisk et al. 2017; Kueppers et al. 2017), while sympatric species like ponderosa pine may simultaneously be favored by such conditions (Rehfeldt et al. 2014; Carroll et al. 2017). In this study, we used a comparative planting experiment of spruce and pine to determine critical first-season (Burdett 1990) survival and growth responses of spruce and pine relative to microsite variables, namely silviculture influences (Grossnickle 2018) including shelter produced by coarse woody debris and by varying levels of canopy cover resulting from regeneration treatments. Based on our findings, we reject our hypotheses for species responses to canopy cover: spruce was not benefitted by greater canopy cover, and pine responded favorably to increased canopy cover, opposite of our hypothesized response. Furthermore, we accept our hypothesis of the benefit of coarse woody debris shelter for spruce, and reject our hypothesis of this benefit for pine only in the most open canopy environments because this effect was beneficial in all canopy environments. For both

species, sensitivity to moisture availability was strongly explained by variation in observed soil moisture, but not by vegetation, litter/debris, or bare soil. As such, we reject our hypothesis of observing covarying influences of ground cover variables but accept that of moisture availability sensitivity. Lastly, we accept our hypothesis that pine displayed greater sensitivity to light availability, and that root growth was favored in intermediate to open canopy environments; however, for pine only we reject our hypothesis of root growth indifference to coarse woody debris shelter. Importantly, in a year in which average growing season temperatures were over 1.5°C higher and precipitation nearly 1/3 lower than the previous thirty-year averages (see *Methods: Study Area*), we expect that our results are especially insightful for showing the sensitivity of these contrasting species to silviculture-induced microsite influences (e.g. Fleming et al. 1998; Newsome et al. 2016) in weather conditions potentially representative of future conditions (Lukas et al. 2014).

1.4.1 Seedling Performance: Survival and Root Biomass

Overall, our results reflect substantial similarities in responses of spruce and pine seedlings to the evaluated microsite effects, suggesting mechanisms common to life-stage, or physiological status of the seedlings (Burdett 1990; Dumroese et al. 2016; Grossnickle 2018), though total pine survival was nearly twice that of spruce. Indeed, with the exception of one additional variable in our spruce survival models, all final candidate survival models for both species included the same suite of microsite variables with similar direction and magnitude of effects. It is likely that these results are representative of a particularly critical period of "coupling" or establishment of planted seedlings to the field environment in the first season following planting (e.g. Grossnickle 2012). Most importantly, the effects of coarse woody debris

shelter were unambiguously beneficial for survival of both species, resulting in almost two times the survival of non-sheltered seedlings. This sheltering effect was by far the strongest of all considered microsite influences for survival but had an opposite and significant effect on root growth only for pine, possibly reflecting light limitations for growth in sheltered treatments. In contrast, the effects of canopy density or openness were largely indistinct relative to other considered microsite influences, though higher density areas slightly favored pine survival. These results regarding canopy influences are likely related to both site-wide moisture availability and availability under canopies of different density (von Arx et al. 2013; Davis et al. 2019). Root growth, however, was significantly greater in canopy environments resulting from silvicultural treatment, at intermediate to low canopy cover, compared to the much more dense, unharvested canopy environment. The lack of canopy effects on the microsite environments influencing survival of our seedlings underscores the relative importance of other microsite variables in our models with more immediate or direct influences on individual seedlings, namely soil moisture and seedling size. While soil moisture was unsurprisingly positively associated with seedling survival, seedling height at planting unexpectedly negatively affected survival for both species, again likely reflecting the stress of severely low moisture availability (e.g. McTague and Tinus 1996; Grossnickle 2005a). Despite these strong similarities in microsite influences among species, it is important to highlight the superior performance of pine, suggesting it is less limited, in terms of absolute outplanting survival rates, by current conditions in low-elevation managed spruce forests like these, especially in warmer and drier years. These results have important implications for adaptive silviculture in similar environments, and in particular highlight the importance of woody debris shelter for reforestation success, the relative

unreliability of predicting success with canopy density, and the potential need to rethink seedling size attributes for planting performance.

The facilitative influence of woody debris shelter in our study was unambiguously important, resulting in nearly twice the survivorship as compared to non-sheltered seedlings of both species (Figures 5 and 8), and predicted probabilities of survivorship 3.5 times greater on average after accounting for other microsite influences in our models (Figures 7 and 10). Though benefits of coarse woody debris for young trees can be many (Harmon et al., 1986; Gray and Spies, 1997), we expect that the primary mechanism of benefit from this shelter to our seedlings was preventing potentially damaging direct radiation from reaching young, succulent stem tissue given the high temperatures and extremely low precipitation during our study. Coarse woody debris can act as a barrier to incoming direct radiation, and so limit the influence of direct radiation and high daytime temperatures on adjacent seedlings and the immediate soil surface (Helgerson 1989; Coop and Schoettle 2009; Maher et al. 2015; Davy 2016). This barrier can limit or prevent exposure of non-hardened, succulent stem tissue of seedlings to the stress of direct radiation (Landis 2010). For young seedlings, protecting succulent tissue from high temperatures may be especially important for preventing cellular damage and subsequent girdling of the stem (Alexander 1984; Seidel 1986), leading to internal physiological failure (Helgerson 1989; Kolb and Robberecht 1996). Furthermore, sheltering influences of coarse woody debris may also be important for lowering ambient air temperatures and consequently raising relative humidity levels at and near the soil surface surrounding the seedling (Castro et al. 2011). Heat-driven evaporation of moisture at the soil surface is reduced by this sheltering effect (Jia-bing et al. 2005; Maher et al. 2015), and availability of moisture to seedlings, necessary for basic physiological processes including transpiration for avoiding heat stress, is consequently

increased (Feller 2003). Our results of positive woody debris shelter influences are generally consistent with documented relationships of regeneration survival or densities with woody debris in environments likely to have high abiotic stress after high-impact disturbance events like intensive harvesting (Alexander 1966; Fajardo et al. 2007) and severe fire (Keyes et al. 2007).

The average size of our coarse woody debris (Table 1) was greater than average heights of pine (+ 3.5 cm) and slightly under those of spruce (- 3.0 cm), which may contribute to explaining the subtle differences for each species with regard to the magnitude of effects of shelter and the contrasting root biomass results for each species. Several studies have documented a superior tolerance of stem tissue to high temperatures ("heat girdling") for ponderosa pine relative to Engelmann spruce (Seidel 1986; Larcher 1995; Kolb and Robberecht 1996). On one hand, the similarity of relative effects of shelter on survival suggested by our models (i.e. the strongest effect in both species models) points to conditions in our study that were in excess (or nearly so) of the relative tolerances thresholds of these species, reducing responses to more basic physiological coping mechanisms for extremely low relative humidity (McTague and Tinus 1996; Grossnickle 2018). However, coarse woody debris shelter improved predicted survival probability for spruce by about 330% on average over unsheltered treatments (Figure 7), but only improved predicted probability of survival for pine by about 150%, with much greater uncertainty on average (Figure 10). This detail of species differences provides some evidence of species-specific responses to shelter and suggests that while coarse woody debris shelter was undoubtedly beneficial for pine survival, this benefit was possibly partially in conflict with the obstruction of light required by pine for growth and survival (e.g. Chen 1997; Sheppard et al. 2006), since sheltered seedlings were on average 3.5 cm shorter than the coarse woody debris. In fact, whereas root growth for spruce, a more shade tolerant species, was not

significantly affected by shelter treatments, pine root growth was significantly greater in unsheltered (no CWD) treatments (Figure 11). In combination, our results thus suggest pine seedlings may have experienced light limitations for growth in sheltered microsites, which in part resulted in less of a change in predicted probability of survival, and greater variability, between sheltered and unsheltered microsites as compared to spruce.

In contrast to the strong and unambiguous positive influence of woody debris shelter for both species, the effects of canopy openness or density, the levels for which were the results of the silvicultural regeneration treatment environment (or absence of), were largely neutral relative to seedling survival in our study. Specifically, canopy effects on spruce survival were unreliable (Figure 6) and had a slight influence on pine survival that was positive with greater canopy cover (density), resulting in a difference in probability of survival of only about 0.08 (~ 27 %) with a change in either direction from mean canopy openness (Figure 10). This curious result (e.g. Nyland 2016) is revealing for the potential mechanisms of canopy influence in these low-elevation spruce stands, which is evidently fundamentally different from the sheltering effects of woody debris, even in (or in part due to) a season of severe abiotic stress. Recent work shows that the effects of canopy buffering influences on sub-canopy environments can be substantial, reducing temperatures by 1.5-5°C on average and consequently considerably reducing vapor pressure deficit, at greater than 50% canopy closure (e.g. von Arx et al. 2013; Davis et al. 2019). Yet these buffering capacities of the forest canopy are significantly dependent on-site moisture status, where drier sites have less to little buffering capacity relative to wetter sites (von Arx et al. 2013; Davis et al. 2019). Additionally, buffering effects are especially acute near the soil surface (<10 cm) rather than above (>2 m) (Davis et al. 2019). We suspect that the potential moderating effects of canopy in our study, especially in terms of facilitating moisture

availability, were largely nonexistent due to the severe moisture deficit during the study period, and because similar mechanisms of buffering, or sheltering influences occurring near the soil surface were otherwise more effectively provided by coarse woody debris (Figures 6 and 9).

Our results for neutral (non-significant) effects of canopy cover for spruce survival (Figure 6), and minor but significant positive effects of canopy cover for pine survival (Figures 9 and 10), both contrary to expectations, possibly suggest diverging tolerance for moisture limitations in denser canopy environments on dry sites. Because spruce is a strongly moisture-dependent species and can thus benefit from, or tolerate, high levels of shade, we expected to see the probability of spruce survival positively influenced by canopy density (Ronco 1967 and 1970; Alexander 1987; Eastham and Jull 1999), especially in drought conditions at a lower-elevation portion of its range (Conlisk et al. 2017; Kueppers et al. 2017). Likewise, we expected pine to respond favorably to less dense canopy environments, especially what we presume to be a relatively productive, higher elevation site for pine (Stein 1988; Chen 1997; Sheppard et al. 2006). However, given our result of positive canopy density influences on pine survival, we suspect that with minimal precipitation received during the study period, what little did occur was likely both intercepted and taken up by established, overstory trees, leaving little moisture available for seedlings especially in denser canopy environments (e.g. Gerhardt 1996; Zou et al. 2008). In fact, our sampling of soil moisture showed significantly lower availability with increasing canopy cover (Table 1). In this way, our pine seedlings, in contrast to spruce, may have been able to benefit more from temperature buffering effects (i.e. shade) of canopy density and simultaneously withstand the relative paucity of moisture in denser canopy areas compared to less dense areas (Stein and Kimberling 2003; Holmgren et al. 2011). Consistent with spruce's relative dependence on moisture and shade tolerance, canopy effects on spruce survival may

have been unclear because spruce simultaneously benefitted from temperature moderation of canopy cover but was equally affected by competition for moisture with canopy trees (e.g. Hill et al. 2018). Additionally, prior evidence for spruce's dependence on regularity of moisture availability, even over total amount (Alexander and Noble 1971; but see Gill et al. 2015), suggest that variability of precipitation in our study period (e.g. zero in June vs. 4 cm in July, data not shown) may have negated the potential for canopy buffering of moisture availability for spruce. Ultimately, these results reflect a trade-off between greater moisture availability and increasing exposure to high temperatures and consequently greater chances of desiccation, or decreased moisture availability and increasing shelter from high temperatures. In this study, pine's capacity to better withstand heat and moisture stress lent to a directional, though minimal, response to this trade-off, while spruce responded similarly to both conditions.

Our results of canopy effects on survival are furthermore consistent with the notion of non-linear, species-specific responses to canopy cover attributable in part to shade and drought tolerance characteristics. In our results, the actual observed difference of canopy environments for mean pine survival and non-survival was only about 2% openness on average, both occurring at intermediate canopy openness values (46% and 48%, respectively). Spruce survivors and non-survivors similarly occurred under intermediate canopy cover levels, separated only by 6% canopy openness on average (52% and 46%, respectively), yet this difference was not significantly influential (Figure 6). In their meta-analysis of species responses to interacting shade and drought effects, Holmgren et al. (2011) report similar non-linear survival results for shade-intolerant species, with possible benefits realized only in intermediate levels of shade (e.g. 40-60% full light), and neutral (i.e. constant, but possibly low degrees of facilitation) results for shade-tolerant species when drought was a driving site factor. However, our models show that

the minimal differences between observed canopy cover for survivors and non-survivors of both species resulted in consequential (or not, for spruce) explanatory relationships for survival variability only after accounting for other effects in the microsite environments of seedlings. For instance, in our dry site conditions, estimating the effects of canopy cover alone could have accounted for differences in the available moisture environment (Table 1; and see, e.g., Gray et al. 2002) and led to significant effects for spruce and pine. Moreover, as suggested above, the strength of effect for coarse woody debris shade, directly adjacent to our seedlings, in both species' survival models here likely account for some of the sheltering influences that canopy cover can provide, since these influences are typically strongest close to the forest floor (Davis et al. 2019). Ultimately, these results reflect potential complications for explaining seedling survival relative to canopy cover, since these relationships can be non-linear and dependent on consideration of species traits and other influences acting on seedling environments, especially those in direct or adjacent proximity to seedlings (e.g. Bonnet et al. 2005). In this way, our results mirror those of previous work on these species which have identified important effects of canopy tree density conditional on covarying site influences (Chen 1997; Lajzerowicz et al 2004; Fajardo et al. 2006; Steen et al. 2008; Newsome et al. 2016; Hill et al. 2018), and which have identified inconclusive canopy effects covarying with stronger relative influences of other variables (Keyes et al .2001; Brang et al. 2003; Bonnet et al. 2005).

The effects of canopy cover on root biomass for survivors of both species showed that root growth on average was significantly restricted in the higher density unharvested environments relative to group-selection and individual-tree selection canopy environments (Figure 11). The difference in canopy cover in each of the three canopy treatments suggests that the competitive influence of canopy cover for light and moisture in these environments occurred

somewhere between the transition from mean openness for unharvested areas (~ 29%) and individual-tree selection treatments, which had on average ~ 50 % openness (Table 1). However, our results suggest that limitations for growth were not significant on average between our treatments beyond this intermediate level of canopy cover in individual-tree selection treatments. Since root growth depends on both light for carbohydrate accumulation and moisture availability to support photosynthesis (Grossnickle 2005a and 2018), the occurrence of lower soil moisture in unharvested treatments likely contributed to these results (Rother et al. 2015). Similar light levels of 25-30% have previously been documented as a threshold of significant reduction in growth potential for spruce (reviewed in Grossnickle 2018). While not explicitly tested in this study, the greater proportion of surviving seedlings, especially spruce, in harvested canopy environments may partially be explained by superior root growth in these environments. Indeed, there is a feedback (Davis and Jacobs 2005; Pinto et al. 2015; Grossnickle 2005a, 2012, and 2018) between moisture availability, root growth, and capacity for uptake of moisture (again for growth, or survival mechanisms like avoiding heat stress) which may have resulted in the qualitative correlation between higher observed survival in harvested areas as compared to unharvested, especially for spruce. While not as evident for pine in our study, prior work has suggested the importance of root growth in longer-term survival of pine after outplanting (e.g. Kolb and Robberchet 1996; Rose et al. 1997).

For pine survival, the competition for resources like light and moisture which we expected to observe with canopy density may in fact be more evident in the negative relationship with surrounding juvenile trees present in our final pine survival model (Figures 9 and 10). Since observed mean juvenile height was only about 3.5 m (Table 1) with a standard deviation of 3.3 m, a one standard deviation decrease from the mean would indicate virtually no present

regeneration. Thus, the standardized effect of mean juvenile height on pine survival suggests the sensitivity of pine survival to presence of other juveniles. We expect that this sensitivity and likely competitive interaction with surrounding juveniles results because the crowns of juvenile trees occupy space, especially shade tolerant conifers, close to the ground and thus to the immediate seedling environment, in contrast to canopy tree crowns which are relatively more separated from seedlings (Coates et al. 2003; Ligot et al. 2014). Crowns closer to individual seedlings are more likely to shade out seedlings, especially the relatively shade-intolerant ponderosa pine (e.g., Ligot et al. 2014), a relationship that logically, as in our model, increases with average height of surrounding juveniles. In addition to shading, surrounding juveniles in our study were likely to have had more established root systems, thus outcompeting our seedlings for limited soil moisture and nutrients (Potvin and Dutilleul 2009; Lei et al. 2012; Zhang et al. 2016). Similar relationships of pine seedlings to larger juveniles (saplings) and canopy trees have been previously described in spatially-explicit relationships, where seedlings densities were negatively associated with saplings and canopy trees at short distances (5 m) (Keyes et al. 2001; but see Fajardo et al. 2006 for contrasting sapling-canopy relations). Yet the distinction of competitive effects on pine survival related to juvenile crowding and overtopping in our results may follow partially from accounting for the positive influences of shelter from coarse woody debris as resulting from non-living features of the microsite environment. Previously documented relationships of adjacent or overtopping vegetation for pine seedling densities and survival have included facilitative (positive; Keyes et al. 2001; Keyes et al. 2009; Puhlick et al. 2012; Ouzts et al. 2015) and competitive (negative; e.g., Callaway et al. 1996; Bonnet et al. 2005). These mixed results, frequently attributed to considerations of moisture availability, suggest that the driving influence of a severe moisture deficit in our study was

exacerbated for pine by juvenile crowding (Keyes et al. 2007; Pinto et al. 2012), especially after accounting for the beneficial influence of shading and moisture retention provided by non-living, non-competitive features of the microsite environment (i.e. facilitation by "dead" shade; Gray and Spies 1997).

Our final survival models indicate that, after accounting for other influences, the probability of survival for both species increased drastically, by approximately 0.50, from lower to higher observed soil moisture conditions (Figures 7 and 10). The strength of this influence, second to that of coarse woody debris for both species, is unsurprising when considering the vital role of soil moisture for tree regeneration, especially for overcoming or avoiding heat stress through transpiration, and supporting basic physiological processes (e.g. Teskey and Hinckley 1986; Grossnickle 2018). In drought conditions, seedling sensitivity to moisture availability is acute (e.g. McDowell et al. 2008; Mucina et al. 2017), and it has been reported that both these species may suffer population declines with warming conditions even with sufficient moisture (Andrus et al. 2018; Conlisk et al. 2017; Kueppers et al. 2017; Rother and Veblen 2017; Petrie et al. 2017). In our study, the similar strength and magnitude of influence of soil moisture evident in survival models for both species (Figures 6 and 9) emphasizes the centrality of soil moisture as a common limiting factor, which may be particularly relevant in the first season after planting, during the process of "coupling" or becoming fully established in the outplanting environment (Grossnickle 2000 and 2005). Comparable importance of seasonal soil moisture availability in benefitting or driving regeneration patterns for these species has been previously reported (e.g., Day 1963; Kolb and Robberecht 1996; Feddema et al. 2013; Rother et al. 2015; Gill et al. 2015). For spruce, the importance of soil moisture may extend in part to the marginally significant positive influence of soil depth in our survival model (Figures 6 and 7). More shallow soils can

restrict water storage and availability (e.g. via runoff; Yanagisawa and Fujita 1999; Kolka and Smidt 2004), especially if precipitation is received in large amounts in few events rather than distributed evenly over the growing season, and can prevent root growth (e.g. Balisky et al. 1995; Shulze et al. 1996). The distinction between pine and spruce in this regard is consistent with qualitative observations the distinction between mature pine and spruce distribution throughout our study area (see *Methods: Experimental Design*).

Seedling height at time of planting also had a significant and strong negative effect on survival of both species in our study (Figures 6 and 9), an influence which roughly doubled predicted survivorship at smaller compared to larger observed height values (Figure 7 and 10). Moreover, both species showed greater sensitivity in predicted survival probability changes to reductions rather than increases in mean observed heights. For spruce (Figure 7), predicted survival was even greater (0.13 change in probability, ~ 120% of the mean predicted probability) with a standard deviation (3.14 cm) decrease from the mean observed height (18.95 cm) versus a stand deviation increase (0.05 change in probability, ~ 45% of the mean). A similar pattern, though not as sensitive, was evident for pine (Figure 10). Seedling size attributes like height and root collar diameter are typically associated with advantages in outplanting environments, especially for the relative advantage of resource (light, moisture, nutrients) acquisition due to more developed root systems and height advantages for outcompeting other vegetation (e.g. Grossnickle 2005b; Pinto et al. 2011; Grossnickle and MacDonald 2018). However, it has also been suggested that these advantages are negated in particularly stressful site conditions (Dumroese et al. 2016; Grossnickle 2012; Pinto et al. 2016), which is presumably the case in our study. From a physiological perspective, seedling survival, where moisture limitations are a particularly prevalent, can be limited by greater aboveground development (e.g. height), since

greater surface area of foliage requires more soil moisture for root systems to support (Stewart and Bernier 1995; Grossnickle 2018). In our results, predicted survival was particularly sensitive to lower ranges of observed heights compared to higher ranges, especially spruce which was taller on average. This suggests a particular sensitivity to and potential benefit of lower ratios of aboveground to belowground development or biomass (e.g. "shoot-to-root" ratios) for outplanting success in dry environments like our study system (Grossnickle 2005a and 2012). Indeed, the use of seedlings with more developed root systems as compared to shoot development has been reported to outperform alternatives in the context of drought stress (e.g. Jurásek et al. 2009). However, we stress that this suggestion of the benefit of lower shoot-to-root ratios is, in this case, a hypothesis for differences which we observed, especially since the seedlings used in this experiment were not intentionally grown for shoot-to-root ratio differences.

1.4.2 Implications for Adaptive Silviculture and Study Limitations

Our results have important implications for reforestation efforts of these species in low-elevation spruce forests in the central Rocky Mountains and in similar treatment environments, and perhaps more broadly for approaches to mixed sympatric species regeneration in marginal distribution areas experiencing climate change. We show the potential value in accounting for a suite of influences in the microsite environments of seedlings in order to better explain and predict survival. Moreover, for seedlings of species with contrasting silvics, such as tolerance of shade and moisture deficits, seedling life-stage and associated physiological status may result in similar relative effects (i.e. strength vis-à-vis other variables) of microsite variables on survival, especially in drought-prone environments in the first season following planting. Yet, while microsite conditions influenced both species with similar relative strength, the results of these

effects were ultimately much more limiting for spruce survival. Ponderosa pine is comparatively better suited overall to current conditions in these low-elevation spruce forests, especially considering anticipated changes toward warmer temperatures and variable precipitation. These results provide evidence for supporting adaptive reforestation efforts which actively incorporate expected species distribution changes resulting from climate change expectations. Specifically, our results imply that reforestation in dry, low-elevation spruce forests in the central-southern Rocky Mountain region should consider the greater likelihood of success of efforts which include transitioning forest cover to species better adapted to future conditions.

With respect to similar relative influences on both species' survival, we provide evidence here for the overwhelming benefit of shelter provided by woody debris or other inanimate objects adjacent to seedlings which drastically improve probability of survival. While planting strategies in western U.S. silviculture often include leveraging the availability of such shelter in post-disturbance outplanting environments (e.g. Landis 2010), our results suggest a change in survival probability that may support more active inclusion of these shelter elements. However, our results also show that important microsite influences may not be reliably approximated by canopy or overstory tree density estimates, since the effects of canopy density on seedling environments is variable with site . In fact, such microsite conditions may be estimated more effectively using variables with more immediate (proximate) effects on individual seedlings, such as woody debris or similar shelter, soil characteristics (i.e., moisture content or water holding capacity), cover of other tree vegetation, and seedling height. Seedling height in particular, has considerable implications for reforestation efforts in similarly stressful (e.g. drought-prone) environments. While nursery practices for drought-hardening seedlings prior to outplanting have provided mixed results in field trials (e.g. Grossnickle 2012; Pinto et al. 2016),

our results suggest that height alone is a major determinant of response to drought conditions for these species. Consequently, our results underscore a hypothesis for the comparative benefit of larger root-to-shoot ratios, or greater belowground investment (root systems, e.g. fibrosity, length, volume; Davis and Jacobs 2005) for outplanting success. For both spruce and pine on harsh sites or in severe drought conditions this hypothesis may apply in particular to the critical period of first-season establishment (Lopushinsky and Beebe 1976).

We have identified important considerations for reforestation in central-southern Rocky Mountain low-elevation subalpine and upper montane forests, especially where anticipated environmental changes include warmer and drier conditions, and reforestation applications include considerations of ponderosa pine and Engelmann spruce. We view our case-study framework as a relevant contribution to the literature, having met a need for field assessments of adaptive silviculture considerations in a specific management context. We also view continued work aimed at identifying microsite influences on regeneration environments within other specific management contexts as essential to expanding empirical support of adaptive management options. Furthermore, better understanding microsite influences on regeneration and reforestation efforts will benefit from additional work which addresses fluctuations in relative effects and species' responses over multiple seasons. While first-season influences which we examined are critical for understanding initial seedling establishment in the outplanting environment, our results do not provide evidence beyond first-season establishment processes.

Lastly, it is important to recognize the remaining uncertainty in our model predictions and resulting classification performance. While our measures of model fit were satisfactory, both species survival models showed mediocre classification ability of observed surviving

seedlings (Tables 2 and 3) at a general 0.50 probability threshold. This suggests that mechanisms of influence captured by our variables were in fact more important to distinguishing between observed survivors and non-survivors, rather than specifically identifying variation in survivors. Very few false positive predictions were present in our models (Tables 2 and 3), a metric which we emphasized in final model selection, indicating strong performance for distinguishing between survivors and non-survivors within model predictions. Indeed, it would not have been useful to develop models which predicted survival given microsite influences which actually resulted in mortality (i.e. false positives). Nonetheless, these results suggest the need for additional work which accounts more precisely for effects explaining variation specifically among survivors. For example, livestock presence in our study area anecdotally accounted for some seedling mortality (estimated ~ 1% of each species), so site characteristics which acted like exclusion mechanisms may have additionally accounted for survival differences in these instances. Additionally, it is possible that our observed levels of canopy openness were not sufficiently broad, on average, to have greater influence on survival responses. Even in the least dense canopy environment of group selection treatments, average openness was only 63% with relatively minimal variation (Table 1). Therefore, for better distinguishing microsite characteristics supporting survival, further work might incorporate additional influences, or potentially address survival-predictor relationships with alternative or supplementary statistical approaches.

1.5 Conclusions

The objective of this study was to determine relative success and predictable microsite relationships for contrasting, sympatric tree species in reforestation efforts of low-elevation

spruce forests that are expected to experience climate warming which would limit the viability of spruce in the future. Our results show that, in drought conditions, pine survival was almost twice that of spruce, but that influences on predicting probability survival for both species were largely similar in relative magnitude and direction of effect. Shelter from coarse woody debris was strongly beneficial for both species and surpassed the strength of influence by all other considered variables. In contrast, the influence of canopy openness or density was largely ambiguous. This result underscores variability in canopy buffering effects on temperature and moisture, which may be greatly reduced on dry sites. Given the severe drought in our study period, our results suggest that canopy cover is an overall unreliable approximation of facilitative or competitive influences for seedling survival (but not for root growth). Rather, effects on survival in our study were linked primarily to variables with more immediate or direct influence on individual seedlings, like woody debris shelter, soil moisture, and seedling height. The negative relationship of predicted survivorship and seedling height for both species may in particular be an informative result for reconsidering the role of seedling size in reforestation success, and specifically emphasizing high ratios of below to aboveground mass for seedlings outplanted to drought-prone environments. In general, the results of our survival models reflect the sensitivity of young, first-season planted seedlings of different species to environmental limitations during a critical period of establishment in the first season after planting. These results can support multi-species reforestation efforts in managed, low-elevation spruce stands in this region with an understanding of influences of silvicultural practices and covarying microsite variables.

REFERENCES

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. and Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1(1), 95-111.

Alexander, R. R., 1966. Stocking of reproduction of spruce-fir clearcuttings in Colorado. USDA For. Serv. Res. Note RM-72.

Alexander, R. R., 1984. Natural regeneration of Engelmann spruce after clearcutting in the central Rocky Mountains in relation to environmental factors. USDA For. Serv. Res. Pap. RM-254.

Alexander, R.R., 1987. Ecology, silviculture, and management of the Engelmann spruce – subalpine fir type in the central and southern Rocky Mountains. USDA For. Serv. Agric. Handb. No. 659.

Alexander, R.R. and Noble, D.L., 1971. Effects of watering treatments on germination, survival, and growth of Engelmann spruce: A greenhouse study USDA For. Serv. Res. Note RM-182.

Alexander, R.R., Troendle, C.A., Kaufmann, M.R., Shepperd, W.D., Crouch, G.L. and Watkins, R.K., 1985. The Fraser Experimental Forest, Colorado: research program and published research 1937-1985. USDA Gen. Tech. Rep. RM-118.

Anderson, P.D. and Puettmann, K.J., 2017. Silviculture for Diverse Objectives. In: Olson D.H., Van Horne B., eds., People, Forests, and Change. Island Press, Washington, DC, pp. 133-148.

Andrus, R.A., Harvey, B.J., Rodman, K.C., Hart, S.J. and Veblen, T.T., 2018. Moisture availability limits subalpine tree establishment. Ecology, 99(3), 567-575.

Astrup, R., Bernier, P.Y., Genet, H., Lutz, D.A. and Bright, R.M., 2018. A sensible climate solution for the boreal forest. Nature Climate Change, 8(1), 1743–1750.

Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Annals of Forest Science, 57(3), 287-301.

Balisky, A.C. and Burton, P., 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. New Forests, 14(1), 63-82.

Balisky, A.C., Salonius, P., Walli, C. and Brinkman, D., 1995. Seedling roots and forest floor: Misplaced and neglected aspects of British Columbia's reforestation effort? The Forestry Chronicle, 71(1), 59-65.

Bates, D., Maechler, M., Bolker, B., and Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.

Bell, D.M., Bradford, J.B. and Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecology and Biogeography, 23(2), 168-180.

Bonnet, V.H., Schoettle, A.W. and Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research, 35(1), 37-47.

Brang, P., Moran, J., Puttonen, P. and Vyse, A., 2003. Regeneration of Picea engelmannii and Abies lasiocarpa in high-elevation forests of south-central British Columbia depends on nurse logs. The Forestry Chronicle, 79(2), 273-279.

Burdett, A.N., 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. Canadian Journal of Forest Research, 20(4), 415-427.

Burnham, K.P. and Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. Springer-Verlag, New York.

Callaway, R.M., 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos, 82(3), 561-573.

Callaway, R.M., DeLucia, E.H., Moore, D., Nowak, R. and Schlesinger, W.H., 1996. Competition and facilitation: contrasting effects of Artemisia tridentata on desert vs. montane pines. Ecology, 77(7), 2130-2141.

Carroll, C.J., Knapp, A.K. and Martin, P.H., 2017. Dominant tree species of the Colorado Rockies have divergent physiological and morphological responses to warming. Forest Ecology and Management, 402, 234-240.

Castro, J., Allen, C.D., Molina-Morales, M., Marañón-Jiménez, S., Sánchez-Miranda, Á. and Zamora, R., 2011. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. Restoration Ecology, 19(4), 537-544.

Chambers, M.E., Fornwalt, P.J., Malone, S.L. and Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine–dominated forests of the Colorado Front Range. Forest Ecology and Management, 378, 57-67.

Chen, H.Y., 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Canadian Journal of Forest Research, 27(9), 1383-1393.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L. and Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. BioScience, 49(4), 288-297.

Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C. and Clair, J.B.S., 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. Forest Ecology and Management, 261(7), 1121-1142.

CFRI (Colorado Forest Restoration Institute), 2017. "Multi-Party Monitoring for the Uncompahgre Plateau Collaborative Forest Landscape Restoration Project." March 2017 Update. Accessed 2/28/19. Available online at: https://cfri.colostate.edu/wp-content/uploads/sites/22/2017/10/2017_UP-CFLRP-MultiPartyMonitoringPlan.pdf

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L. and Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. Forest Ecology and Management, 186(1-3), 297-310.

Conlisk, E., Castanha, C., Germino, M.J., Veblen, T.T., Smith, J.M. and Kueppers, L.M., 2017. Declines in low-elevation subalpine tree populations outpace growth in high-elevation populations with warming. Journal of Ecology, 105(5), 1347-1357.

Coop, J.D. and Schoettle, A.W., 2009. Regeneration of Rocky Mountain bristlecone pine (Pinus aristata) and limber pine (Pinus flexilis) three decades after stand-replacing fires. Forest Ecology and Management, 257(3), 893-903.

Copenhaver-Parry, P.E., Shuman, B.N. and Tinker, D.B., 2017. Toward an improved conceptual understanding of North American tree species distributions. Ecosphere, 8(6), e01853. 10.1002/ecs2.1853.

Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E. and Abatzoglou, J.T., 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography, 42(1), 1-11.

Davis, A.S. and Jacobs, D.F., 2005. Quantifying root system quality of nursery seedlings and relationship to outplanting performance. New Forests, 30(2-3), 295-311.

Davy, R., 2016. Impacts of coarse woody debris and edge effects on Engelmann spruce regeneration. Thesis, Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colo.

Day, R.J., 1963. Spruce seedling mortality caused by adverse summer microclimate in the Rocky Mountains. Publications. Department of Forests, Canada, Pub. No. 1003.

Day, R.J., 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. Department of Forests, Canada, Pub. No. 1037.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J. and Decocq, G.M., 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences, 110(46), 18561-18565.

DeRose, R.J. and Long, J.N., 2014. Resistance and resilience: A conceptual framework for silviculture. Forest Science, 60(6), 1205-1212.

Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K. and Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography, 24(8), 917-927.

Dodson, E.K. and Root, H.T., 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. Forest Ecology and Management, 302, 163-170.

Dumroese, K.R., Landis, T.D., Pinto, J.R., Haase, D.L., Wilkinson, K.W. and Davis, A.S., 2016. Meeting forest restoration challenges: using the target plant concept. Reforesta, 1(1), 37-52.

Eastham, A.M. and Jull, M.J., 1999. Factors affecting natural regeneration of Abies lasiocarpa and Picea engelmannii in a subalpine silvicultural systems trial. Canadian Journal of Forest Research, 29(12), 1847-1855.

Elsen, P.R. and Tingley, M.W., 2015. Global mountain topography and the fate of montane species under climate change. Nature Climate Change, 5(8), 772.

Fahey, R.T., Alveshere, B.C., Burton, J.I., D'Amato, A.W., Dickinson, Y.L., Keeton, W.S., Kern, C.C., Larson, A.J., Palik, B.J., Puettmann, K.J. and Saunders, M.R., 2018. Shifting conceptions of complexity in forest management and silviculture. Forest Ecology and Management, 421, 59-71.

Fajardo, A., Graham, J.M., Goodburn, J.M. and Fiedler, C.E., 2007. Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA. Forest Ecology and Management, 243(1), 50-60.

Feddema, J.J., Mast, J.N. and Savage, M., 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. Ecological Modelling, 253, 56-69.

Fay, M., and Shaw, P., 2010. Exact and Asymptotic Weighted Logrank Tests for Interval Censored Data: The interval R Package. Journal of Statistical Software, 36(2), 1-34.

Fawcett, T., 2006. An introduction to ROC analysis. Pattern Recognition Letters, 27(8), 861-874.

Feller, M.C., 1998. Influence of ecological conditions on Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) germinant survival and initial seedling growth in south-central British Columbia. Forest Ecology and Management, 107(1-3), 55-69.

Feller, M.C., 2003. Coarse woody debris in the old-growth forests of British Columbia. Environmental Reviews, 11(S1), S135-S157.

Fischer, A.P., 2018. Forest landscapes as social-ecological systems and implications for management. Landscape and Urban Planning, 177, 138-147.

Fleming, R.L., Black, T.A., Adams, R.S. and Stathers, R.J., 1998. Silvicultural treatments, microclimatic conditions and seedling response in Southern interior clearcuts. Canadian Journal of Soil Science, 78(1), 115-126.

Fox J., and Weisberg, S., 2018. “Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals.” Journal of Statistical Software, 87(9), 1–27.

Frazer, G.W., Trofymow, J.A. and Lertzman, K.P., 1997. A method for estimating canopy openness, effective leaf area index, and photosynthetically active photon flux density using hemispherical photography and computerized image analysis techniques. Canadian Forest Service, Information Report BC-X-373.

Gerhardt, K., 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. Forest Ecology and Management, 82(1-3), 33-48.

Germino, M.J., Smith, W.K. and Resor, A.C., 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology, 162(2), 157-168.

Gill, R.A., Campbell, C.S. and Karlinsey, S.M., 2015. Soil moisture controls Engelmann spruce (Picea engelmannii) seedling carbon balance and survivorship at timberline in Utah, USA. Canadian Journal of Forest Research, 45(12), 1845-1852.

Glatthorn, J. and Beckschäfer, P., 2014. Standardizing the protocol for hemispherical photographs: accuracy assessment of binarization algorithms. PLoS One, 9(11): e111924.

Golladay, S.W., Martin, K.L., Vose, J.M., Wear, D.N., Covich, A.P., Hobbs, R.J., Klepzig, K.D., Likens, G.E., Naiman, R.J. and Shearer, A.W., 2016. Achievable future conditions as a framework for guiding forest conservation and management. Forest Ecology and Management, 360, 80-96.

Gray, A.N. and Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology, 78(8), 2458-2473.

Gray, A.N., Spies, T.A. and Easter, M.J., 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research, 32(2), 332-343.

Grossnickle, S.C., 2005a. Importance of root growth in overcoming planting stress. New Forests, 30(2-3), 273-294.

Grossnickle, S.C., 2005b. Seedling Size and Reforestation Success How Big is Big Enough? In: Colombo, S.J., ed. The Thin Green Line : a symposium on the state-of-the-art in reforestation: proceedings. Queen's Printer for Ontario, Ontario, Canada., 138-143.

Grossnickle, S.C., 2012. Why seedlings survive: influence of plant attributes. New Forests, 43(5-6), 711-738.

Grossnickle, S., 2018. Seedling Establishment on a Forest Restoration Site. Reforesta, (6), 110-139.

Grossnickle, S.C. and MacDonald, J.E., 2018. Why seedlings grow: influence of plant attributes. New Forests, 49(1), 1-34.

Guldin, J.M., 2019. Silvicultural options in forests of the southern United States under changing climatic conditions. New Forests, 50(1), 71-87.

Hall, R.J., Côté, J.F., Mailly, D. and Fournier, R.A., 2017. Comparison of software tools for analysis of hemispherical photographs. In: Fournier R., Hall, R., eds. Hemispherical

Photography in Forest Science: Theory, Methods, Applications, , (28), 187-226. Springer, Dordrecht.

Halofsky, J.E., Andrews-Key, S.A., Edwards, J.E., Johnston, M.H., Nelson, H.W., Peterson, D.L., Schmitt, K.M., Swanston, C.W. and Williamson, T.B., 2018. Adapting forest management to climate change: The state of science and applications in Canada and the United States. Forest Ecology and Management, 421, 84-97.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R. and Lienkaemper, G.W., 1986. Ecology of coarse woody debris in temperate ecosystems. In Advances in Ecological Research, (15), 133-302.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E., Robinson, B.S., Hodgson, D.J. and Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ, 6, e4794.

Hedge, C.E., Peterman, Z.E., Case, J.E. and Obradovich, J.D., 1968. Precambrian geochronology of the northwestern Uncompahgre Plateau, Utah and Colorado. US Geological Survey Professional Paper 600, C91-96.

Helgerson, O.T., 1989. Heat damage in tree seedlings and its prevention. New Forests, 3(4), 333-358.

Hill, E., Ex, S., Aldridge, C. and Prolic, C., 2018. Overstory density, short growing seasons, and moisture limit Engelmann spruce establishment over time in high-elevation managed stands. Canadian Journal of Forest Research, 49(1), 64-75.

Hof, A.R., Dymond, C.C. and Mladenoff, D.J., 2017. Climate change mitigation through adaptation: the effectiveness of forest diversification by novel tree planting regimes. Ecosphere, 8(11), e01981.

Holmgren, M., Gómez-Aparicio, L., Quero, J.L. and Valladares, F., 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia, 169(2), 293-305.

Hughes, T., Kingston, R., and Cencich, B. 1995. Soil survey of Uncompahgre National Forest area, Colorado, parts of Mesa, Montrose, Ouray, and San Miguel counties. USDA Forest Service and Soil Conservation Service, Washington, DC.

Ibáñez, I., Clark, J.S., LaDeau, S. and Lambers, J.H.R., 2007. Exploiting temporal variability to understand tree recruitment response to climate change. Ecological Monographs, 77(2), 163-177.

Jacobs, D.F. and Steinbeck, K., 2001. Tree shelters improve the survival and growth of planted Engelmann spruce seedlings in southwestern Colorado. Western Journal of Applied Forestry, 16(3), 114-120.

Jacobs, D.F., Oliet, J.A., Aronson, J., Bolte, A., Bullock, J.M., Donoso, P.J., Landhäusser, S.M., Madsen, P., Peng, S., Rey-Benayas, J.M. and Weber, J.C., 2015. Restoring forests: what constitutes success in the twenty-first century? New Forests, 46(5-6), 601-614.

Jia-bing, W., De-xin, G., Shi-jie, H., Mi, Z. and Chang-Jie, J., 2005. Ecological functions of coarse woody debris in forest ecosystem. Journal of Forestry Research, 16(3), 247-252.

Jurásek, A., Leugner, J. and Martincová, J., 2009. Effect of initial height of seedlings on the growth of planting material of Norway spruce (Picea abies [L.] Karst.) in mountain conditions. Journal of Forest Science, 55(3), 112-118.

Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review. Annals of Forest Science, 72(2), 145-167.

Kemp, K. B., J. J. Blades, P. Z. Klos, T. E. Hall, J. E. Force, P. Morgan, and W. T. Tinkham. 2015. Managing for climate change on federal lands of the western United States: perceived usefulness of climate science, effectiveness of adaptation strategies, and barriers to implementation. Ecology and Society 20(2): 17.

Keyes, C.R., Acker, S.A., and Greene, S.E., 2001. Overstory and shrub influences on seedling recruitment patterns in an old-growth ponderosa pine stand. Northwest Science, 75(3), 204-210.

Keyes, C.R., Maguire, D.A. and Tappeiner, J.C., 2007. Observed dynamics of ponderosa pine (Pinus ponderosa var. ponderosa Dougl. ex Laws.) seedling recruitment in the Cascade Range, USA. New Forests, 34(1), 95-105.

Keyes, C.R., Maguire, D.A. and Tappeiner, J.C., 2009. Recruitment of ponderosa pine seedlings in the Cascade Range. Forest Ecology and Management, 257(2), 495-501.

Kolb, P.F. and Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa seedlings. Tree Physiology, 16(8), 665-672.

Kolka, R.K. and Smidt, M.F., 2004. Effects of forest road amelioration techniques on soil bulk density, surface runoff, sediment transport, soil moisture and seedling growth. Forest Ecology and Management, 202(1-3), 313-323.

Kroiss, S.J. and HilleRisLambers, J., 2015. Recruitment limitation of long-lived conifers: implications for climate change responses. Ecology, 96(5), 1286-1297.

Kueppers, L.M., Conlisk, E., Castanha, C., Moyes, A.B., Germino, M.J., De Valpine, P., Torn, M.S. and Mitton, J.B., 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology, 23(6), 2383-2395.

Lajzerowicz, C.C., Walters, M.B., Krasowski, M. and Massicotte, H.B., 2004. Light and temperature differentially colimit subalpine fir and Engelmann spruce seedling growth in partial-cut subalpine forests. Canadian Journal of Forest Research, 34(1), 249-260.

Larson, J.E. and Funk, J.L., 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. Journal of Ecology, 104(5), 1284-1298.

Landis, T.D., 2010. The container tree nursery manual: seedling processing, storage, and outplanting. USDA For. Serv. Agric. Handb. No. 674.

Lawrence, A., 2017. Adapting through practice: Silviculture, innovation and forest governance for the age of extreme uncertainty. Forest Policy and Economics, 79, 50-60.

Lei, P., Scherer-Lorenzen, M. and Bauhus, J., 2012. Belowground facilitation and competition in young tree species mixtures. Forest Ecology and Management, 265, 191-200.

Lembrechts, J.J., Nijs, I. and Lenoir, J., 2018. Incorporating microclimate into species distribution models. Ecography, 1-23.

Ligot, G., Balandier, P., Courbaud, B., Jonard, M., Kneeshaw, D. and Claessens, H., 2014. Managing understory light to maintain a mixture of species with different shade tolerance. Forest Ecology and Management, 327, 189-200.

Lopushinsky, W. and Beebe, T., 1976. Relationship of shoot-root ration to survival and growth of outplanted Douglas-fir and ponderosa pine seedlings. USDA For. Serv. Res. Pap. PNW-274.

Lukas, J., Barsugli, J., Doesken, N., Rangwala, I., and Wolter, K. 2014. Climate Change in Colorado: A Synthesis to Support Water Resources Management and Adaptation. A Report for the Colorado Water Conservation Board, University of Colorado Boulder, Western Water Assessment, Cooperative Institute for Research in Environmental Sciences (CIRES).

Salvatore M., 2019. rcompanion: Functions to Support Extension Education Program Evaluation. R package version 2.0.10. https://CRAN.R-project.org/package=rcompanion

Maher, C.T., Barber, A.L. and Affleck, D.L., 2015. Shelter provided by wood, facilitation, and density-dependent herbivory influence Great Basin bristlecone pine seedling survival. Forest Ecology and Management, 342, 76-83.

Máliš, F., Kopecký, M., Petřík, P., Vladovič, J., Merganič, J. and Vida, T., 2016. Life stage, not climate change, explains observed tree range shifts. Global Change Biology, 22(5), 1904-1914.

Matonis, M.S., Binkley, D., Franklin, J. and Johnson, K.N., 2016. Benefits of an "undesirable" approach to natural resource management. Journal of Forestry, 114(6), 658-665.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G. and Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. New Phytologist, 178(4), 719-739.

McTague, J.P. and Tinus, R.W., 1996. The effects of seedling quality and forest site weather on field survival of ponderosa pine. Tree Planters Notes, 47, 16-23.

Messier, C., Puettmann, K., Filotas, E. and Coates, D., 2016. Dealing with non-linearity and uncertainty in forest management. Current Forestry Reports, 2(2), 150-161.

Mok, H.F., Arndt, S.K. and Nitschke, C.R., 2012. Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. Global Change Biology, 18(3), 1053-1072.

Mucina, L., Bustamante-Sánchez, M.A., Duguy, B., Holmes, P., Keeler-Wolf, T., Armesto, J.J., Dobrowolski, M., Gaertner, M., Smith-Ramírez, C. and Vilagrosa, A., 2017. Ecological restoration in mediterranean-type shrublands and woodlands. In: Allison, S. & Murphy, S., eds., Routledge Handbook of Ecological and Environmental Restoration. Taylor & Francis, Abingdon, UK, 173-196.

Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., Janowiak, M.K., Powers, M.P., Joyce, L.A., Millar, C.I. and Peterson, D.L., 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. Journal of Forestry, 115(3), 167-178.

Newsome, T.A., Brown, K.R. and Nemec, A.F.L., 2016. Effects of opening size and microsite on performance of planted tree seedlings in high-elevation Engelmann spruce–subalpine fir forests managed as mountain caribou habitat in British Columbia. Forest Ecology and Management, 370, 31-44.

Nolan, R.H., Drew, D.M., O'Grady, A.P., Pinkard, E.A., Paul, K., Roxburgh, S.H., Mitchell, P.J., Bruce, J., Battaglia, M. and Ramp, D., 2018. Safeguarding reforestation efforts against changes in climate and disturbance regimes. Forest Ecology and Management, 424, 458-467.

Nolet, P., Kneeshaw, D., Messier, C. and Béland, M., 2018. Comparing the effects of even-and uneven-aged silviculture on ecological diversity and processes: A review. Ecology and Evolution, 8(2), 1217-1226.

North, M.P., Stevens, J.T., Greene, D.F., Coppoletta, M., Knapp, E.E., Latimer, A.M., Restaino, C.M., Tompkins, R.E., Welch, K.R., York, R.A. and Young, D.J., 2019. Tamm Review: Reforestation for resilience in dry western US forests. Forest Ecology and Management, 432, 209-224.

Nyland, R.D., 2016. Silviculture: concepts and applications. 3rd ed. Waveland Press, Long Grove, IL.

Ouzts, J., Kolb, T., Huffman, D. and Meador, A.S., 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. Forest Ecology and Management, 354, 281-290.

Petrie, M.D., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., Andrews, C.M. and Schlaepfer, D.R., 2017. Climate change may restrict dryland forest regeneration in the 21st century. Ecology, 98(6), 1548-1559.

Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M. and Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. Forest Ecology and Management, 361, 328-338.

Pinto, J.R., Marshall, J.D., Dumroese, R.K., Davis, A.S. and Cobos, D.R., 2011. Establishment and growth of container seedlings for reforestation: A function of stocktype and edaphic conditions. Forest Ecology and Management, 261(11), 1876-1884.

Pinto, J.R., Marshall, J.D., Dumroese, R.K., Davis, A.S. and Cobos, D.R., 2012. Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. Canadian Journal of Forest Research, 42(2), 333-344.

Pinto, J.R., Marshall, J.D., Dumroese, R.K., Davis, A.S. and Cobos, D.R., 2016. Seedling establishment and physiological responses to temporal and spatial soil moisture changes. New Forests, 47(2), 223-241.

Potvin, C. and Dutilleul, P., 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. Ecology, 90(2), 321-327.

Puhlick, J.J., Laughlin, D.C. and Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. Forest ecology and management, 264, 10-19.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecology Letters, 3(4), 349-361.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rehfeldt, G.E., Jaquish, B.C., López-Upton, J., Sáenz-Romero, C., St Clair, J.B., Leites, L.P. and Joyce, D.G., 2014. Comparative genetic responses to climate for the varieties of Pinus ponderosa and Pseudotsuga menziesii: Realized climate niches. Forest Ecology and Management, 324, 126-137.

Rehfeldt, G.E., Worrall, J.J., Marchetti, S.B. and Crookston, N.L., 2015. Adapting forest management to climate change using bioclimate models with topographic drivers. Forestry: An International Journal of Forest Research, 88(5), 528-539.

Ronco, F., 1967. Lessons from artificial regeneration studies in a cutover beetle-killed spruce stand in western Colorado. USDA For. Serv. Res. Note RM-90.

Ronco, F., 1970. Influence of high light intensity on survival of planted Engelmann spruce. Forest Science, 16(3), 331-339.

Rose, R., Haase, D.L., Kroiher, F. and Sabin, T., 1997. Root volume and growth of ponderosa pine and Douglas-fir seedlings: a summary of eight growing seasons. Western Journal of Applied Forestry, 12(3), 69-73.

Rother, M.T. and Veblen, T.T., 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere, 7(12), e01594.

Rother, M. and Veblen, T., 2017. Climate drives episodic conifer establishment after fire in dry ponderosa pine forests of the Colorado Front Range, USA. Forests, 8(5), 159.

Rother, M.T., Veblen, T.T. and Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Canadian Journal of Forest Research, 45(11), 1607-1616.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J., and Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics, 12, 77.

Saxton, K.E. and Rawls, W.J., 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Science Society of America Journal, 70(5), 1569-1578.

Seidel, K.W., 1986. Tolerance of seedlings of ponderosa pine. Douglas-fir, grand fir, and engelmann spruce for high temperatures. Northwest Science, 60(1), 1-7.

Shepperd, W.D., Edminster, C.B. and Mata, S.A., 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. Western Journal of Applied Forestry, 21(1), 19-26.

Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M. and Ehleringer, J.R., 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia, 108(3), 503-511.

Sousa-Silva, R., Verbist, B., Lomba, Â., Valent, P., Suškevičs, M., Picard, O., Hoogstra-Klein, M.A., Cosofret, V.C., Bouriaud, L., Ponette, Q. and Verheyen, K., 2018. Adapting forest management to climate change in Europe: Linking perceptions to adaptive responses. Forest Policy and Economics, 90, 22-30.

Spittlehouse, D.L., 2005. Integrating climate change adaptation into forest management. The Forestry Chronicle, 81(5), 691-695.

Stein, S.J., 1988. Explanations of the imbalanced age structure and scattered distribution of ponderosa pine within a high-elevation mixed coniferous forest. Forest Ecology and Management, 25(2), 139-153.

Stein, S.J. and Kimberling, D.N., 2003. Germination, establishment, and mortality of naturally seeded southwestern ponderosa pine. Western Journal of Applied Forestry, 18(2), 109-114.

Stewart, J.D. and Bernier, P.Y., 1995. Gas exchange and water relations of 3 sizes of containerized Picea mariana seedlings subjected to atmospheric and edaphic water stress under controlled conditions. Annals of Forest Science, 51(1), 1-9.

Teskey, R.O. and Hinckley, T.M., 1986. Moisture: effects of water stress on trees. In: Hennessey T.C., Dougherty P.M., Kossuth S.V., Johnson J.D., eds. Stress physiology and forest productivity. Forestry Sciences, (21), 9-33. Springer, Dordrecht

USDA FS (Forest Service), 2002. Chapter 2 – Reforestation. In FSH 2409.17 – Silvicultural Practices Handbook. Forest Service Handbook Southwestern Region (Region 3), Albuquerque, New Mexico. Supplement No. R3 2409.17-2002-1.

USDA NRCS (Natural Resources Conservation Service) GeoSpatial Data Gateway, 2018. Montrose County, Colorado. Accessed on February 15, 2018.

von Arx, G., Graf Pannatier, E., Thimonier, A. and Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. Journal of Ecology, 101(5), 1201-1213.

Yanagisawa, N. and Fujita, N., 1999. Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. Ecological Research, 14(2), 165-177.

Yousefpour, R., Temperli, C., Jacobsen, J.B., Thorsen, B.J., Meilby, H., Lexer, M., Lindner, M., Bugmann, H., Borges, J., Palma, J. and Ray, D., 2017. A framework for modeling adaptive forest management and decision making under climate change. Ecology and Society, 22(4).

Zhang, Z., Papaik, M.J., Wang, X., Hao, Z., Ye, J., Lin, F. and Yuan, Z., 2016. The effect of tree size, neighborhood competition and environment on tree growth in an old-growth temperate forest. Journal of Plant Ecology, 10(6), 970-980.

Zou, C.B., Breshears, D.D., Newman, B.D., Wilcox, B.P., Gard, M.O. and Rich, P.M., 2008. Soil water dynamics under low-versus high-ponderosa pine tree density: ecohydrological functioning and restoration implications. Ecohydrology, 1(4), 309-315.